UNITED STATES DEPARTMENT OF AGRICULTURE

In Cooperation with the
Montana Agricultural Experiment Station

DEPARTMENT BULLETIN No. 1403

Washington, D. C. ▼ May, 1926

SEGREGATION AND CORRELATED INHERITANCE IN MARQUIS AND HARD FEDERATION CROSSES, WITH FACTORS FOR YIELD AND QUALITY OF SPRING WHEAT IN MONTANA

By

J. ALLEN CLARK, Agronomist in Charge, and JOHN R. HOOKER, Scientific Aid,
Western Wheat Investigations, Office of Cereal Crops and Diseases,
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WASHINGTON
GOVERNMENT PRINTING OFFICE
1926

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CONTENTS

LARGER YIELDS OF WHEAT WITH PRESENT QUALITY DESIRED

The profitable production of hard red spring wheat on the dry lands of Montana is dependent in part upon improvement in yield of the varieties grown. At present Marquis is the leading commercial spring wheat of the State. Under favorable conditions it is a high-yielding variety, but under conditions of deficient moisture Marquis is not adapted sufficiently to produce profitable crops. In unfavorable seasons and in large sections having limited rainfall, therefore, spring-wheat production often is unprofitable in Montana, partly because of dependence on this or any other available variety.

The quality of Marquis is satisfactory. The low-yielding Marquis grown on the Montana dry lands is especially high in quality and much desired by the grain trade. The problem is therefore to

[1] The Montana Agricultural Experiment Station cooperated in these investigations. Acknowledgment is gladly given here for field assistance rendered by M. A. Bell at Bozeman (1923) and Havre (1924), R. W. May at Moccasin, and J. L. Carter at Bozeman (1924). The writers also wish to express appreciation to Sewall Wright, of the Bureau of Animal Industry, United States Department of Agriculture, for advice given in the genetic and statistical analysis of the data.

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improve the yield and maintain the quality. In order to do this it is necessary to determine the factors which make for yield and quality under different Montana conditions and to develop a new variety of equal quality which will increase average yields.

MATERIAL AND METHODS

Unfavorable results with wheat production in Montana are almost entirely the result of drought. A new variety must be drought escaping or drought resistant in order to meet most successfully the prevailing conditions. The choice of an early drought-resistant high-yielding variety for crossing with Marquis and the selection of representative locations for testing the progeny in Montana were the problems of first consideration in developing a breeding program.

PARENT MATERIAL

The Hard Federation was selected for crossing with Marquis, as it appeared the best available variety at the time this study was projected. It had been included in varietal experiments at Moccasin, Mont., in 1920, and had outyielded Marquis by 7.7 bushels per acre. Its earliness, drought resistance, and high-yielding ability had been observed in Oregon and California and reported by Clark, Stephens, and Florell (*6*).[2] The crosses were made in 1921, in which year Hard Federation was first included in varietal experiments at Bozeman and Havre, Mont., and at numerous stations in other States.

Marquis and Hard Federation have several contrasting morphological and quantitative characters, some of which affect differently their adaptation in certain localities and seasons. Marquis is a midseason, midtall variety with awnletted spikes, flat leaves, white glumes, and hard red kernels. Hard Federation is an early, short variety with awnless spikes, curling leaves, brown glumes, and hard white kernels. The inheritance of these contrasting characters and their effect, if any, on the yield and quality of the product under different Montana conditions have been studied.

Crude-protein content has been selected among several quality factors as the one most important, as it is directly reflected in the price of wheat when marketed. At present a premium is paid for hard red spring wheat of 5 to 10 cents a bushel for each per cent of crude protein above 12. Other quality factors are important but are more difficult to measure in the small quantity of seed available in hybrid material.

To show the comparative quality of the two parents, data from milling and baking experiments which have been conducted by the United States Department of Agriculture with comparable samples of Hard Federation and Marquis wheats during the seven years from 1918 to 1924, inclusive, are given in Table 1. The data show that Hard Federation compares favorably with Marquis in all factors. This result agrees with that of earlier experiments reported by Shollenberger and Clark (*17*), which show Hard Federation to be one of the best varieties for bread making in the white class. It has no important objectionable feature when compared with Marquis, recognized as the leading variety for milling and bread making.

[2] The serial numbers (*italic*) in parentheses refer to "Literature cited" at the end of this bulletin.

TABLE 1.—*Summary of milling and baking data from 69 comparable samples of Hard Federation and Marquis wheats grown during the seven years from 1918 to 1924, inclusive* [1]

Descriptive data	Comparable samples		
	Hard Federation	Marquis	Percentage of Marquis
Number of samples	69	69	
Bushel weight, pounds	58.9	59.1	99.7
Crude-protein content of wheat [2], per cent	13.3	13.7	97.1
Yield of straight flour, do	71.7	73.2	98.0
Yield of shorts, do	15.3	14.2	107.7
Yield of bran, do	14.3	14.8	96.6
Water absorption of flour, do	62.7	60.5	103.6
Volume of loaf, cubic centimeters	2,165	2,222	97.4
Weight of loaf, grams	507	502	101.0
Texture of loaf, per cent	89.5	89.1	100.4
Color of loaf, do	92.4	91.4	101.1
Ash in flour, do	[3].47	[3].50	94.0

[1] Experiments conducted by the Milling Investigations Section, Grain Division, Bureau of Agricultural Economics.
[2] N×5.7; basis, 13.5 per cent moisture.
[3] Only 68 samples.

Since 1920 numerous agronomic data also have been accumulated which afford a basis for comparing the parental varieties. The data for six quantitative characters concerned in this inheritance study, from varietal experiments in plats at Bozeman, Moccasin, and Havre, Mont., are given in Table 2.

The data in Table 2 show that Hard Federation heads at a considerably earlier date than Marquis under all three environmental conditions and that it ripens but slightly earlier and sometimes as late or later. This results in a fruiting period, or number of days from heading to ripening, longer for Hard Federation than for Marquis. The length of the fruiting period also varies with the season, and the season producing the longer fruiting period appears to be associated with higher yield. Marquis is shown to be considerably taller (pl. 1) than Hard Federation, and greater height within each variety seems to be directly associated with larger yields.

That comparative yields of the two varieties differ greatly in certain seasons may be due in part to the opposing advantages of a long fruiting period and of the growth factors which develop plant height. On the average, Hard Federation has slightly outyielded Marquis at Bozeman and Moccasin, but not at Havre. However, the lower yields of Hard Federation under the unfavorable conditions at Havre seem to be due more to damage from weeds (Russian thistles) than to its earliness or lack of drought resistance. The short stems and curling leaves of Hard Federation render it less adapted than Marquis to compete with weed growth. In the nursery at Havre, where weed growth was destroyed, Hard Federation produced the higher yields.

The crude-protein content of the two varieties also differs greatly in certain seasons, with Marquis on the average exceeding Hard Federation at two of the three stations. High crude-protein content appears to be somewhat associated with low yields.

Correlation studies of these various factors in the progeny of hybrids of the two varieties will more definitely determine the amount

of association. Through the testing of large numbers of selections made on the basis of these correlations it is hoped to develop a new variety better adapted than either parent to Montana conditions.

TABLE 2.—*Annual and average date of heading and ripening, fruiting period, height, yield, and crude-protein content of Marquis and Hard Federation wheats grown in plat experiments at Bozeman, Moccasin, and Havre, Mont., during the five years from 1920 to 1924, inclusive*

Station, variety, and year	Date headed	Date ripe	Fruiting period (days)	Height (inches)	Yield per acre (bushels)	Crude protein (N×5.7) (per cent)
BOZEMAN						
Marquis:						
1921	July 16	Aug. 20	35	47	41.1	13.1
1922	July 19	Aug. 30	42	50	60.6	10.5
1923	July 17	Sept. 3	48	48	52.3	13.4
1924	July 14	Sept. 9	57	38	38.7	10.7
Average	July 17	Aug. 31	46	46	48.2	11.9
Hard Federation:						
1921	July 9	Aug. 20	42	36	58.7	14.6
1922	July 14	Aug. 28	45	40	62.7	12.5
1923	July 11	Sept. 4	55	40	48.4	12.8
1924	July 13	Sept. 2	51	28	24.6	9.9
Average	July 12	Aug. 29	48	36	48.6	12.5
MOCCASIN						
Marquis:						
1920	July 26	Aug. 22	27	35	23.1	14.8
1921	July 10	Aug. 11	32	41	28.3	14.5
1922	July 20	Aug. 16	27	38	27.3	14.6
1923	July 18	Aug. 23	36	39	24.6	14.3
1924	July 17	Aug. 24	38	39	32.0	14.5
Average	July 18	Aug. 19	32	38	27.1	14.5
Hard Federation:						
1920	July 19	Aug. 26	38	35	30.8	13.5
1921	July 1	Aug. 8	38	31	32.1	12.8
1922	July 10	Aug. 14	35	33	34.2	14.3
1923	July 10	Aug. 17	38	32	17.1	12.7
1924	July 12	Aug. 18	37	37	31.5	13.6
Average	July 10	Aug. 17	37	34	29.1	13.4
HAVRE						
Marquis:						
1921	----------	July 25	----------	23	11.7	17.6
1922	----------	Aug. 14	----------	19	5.8	15.5
1923	July 15	Aug. 14	30	36	20.3	13.8
1924	July 9	Aug. 10	32	26	12.3	12.9
Average	July 12	[1] Aug. 12	31	26	12.5	15.0
Hard Federation:						
1921	----------	July 23	----------	18	10.8	16.1
1922	----------	Aug. 1	----------	12	5.2	14.6
1923	July 13	Aug. 17	35	30	10.8	12.8
1924	July 4	Aug. 8	35	26	11.7	13.1
Average	July 9	[1] Aug. 13	35	22	9.6	14.2

[1] Average of 1923 and 1924 data only.

METHODS USED

Under a cooperative agreement with the Montana Agricultural Experiment Station the hybrid material was grown at the three stations previously mentioned, these stations being fairly representative of nonirrigated conditions in both the intermountain and Plains sections for wheat production in Montana.

Bozeman is located under fairly humid conditions in the Gallatin Valley and has a normal annual precipitation of 18.67 inches. Moc-

casin is located under semiarid or average dry-land conditions in the Judith Basin and has a normal annual precipitation of 16.51 inches. Havre is under marginal dry-farming conditions in the so-called "Triangle" section and has a normal annual precipitation of but 13.71 inches. Thus, three distinct environmental conditions are represented.

The Marquis × Hard Federation and reciprocal crosses here studied were made, at the request of the senior writer, by V. H. Florell (*8*) at Chico, Calif., in May, 1921. The F_1 material was grown at Davis, Calif., in 1922. The Marquis ♀ × Hard Federation ♂ crosses were given the hybrid number 21202 and the Hard Federation ♀ × Marquis ♂ crosses number 21203. The first two numerals, 21, stand for the year 1921, in which the crosses were made. The numbers 202 and 203 were assigned to these particular crosses. The F_1 material was divided. Families 21202 B1, B2, and B3 and 21203 A1, A2, and A3 were sent to Bozeman, Mont., and families 21202 A1, A2, and A3 and 21203 C1, C2, and C3 were sent to Moccasin, Mont., where the 12 F_2 families were grown in 1923.

In 1923 the hybrid plants at both Bozeman and Moccasin were definitely spaced at 3-inch intervals in rod rows 1 foot apart. Unfortunately, the parent varieties were not sown at Moccasin. At Bozeman the Hard Federation parent was sown identically with the hybrids, but the Marquis parent was sown two days later and under slightly different conditions.

In 1924 the F_3 material was grown at Bozeman, Moccasin, and Havre in nursery rows 1 foot apart. At Bozeman 70 kernels were spaced 3 inches apart in each row. At Havre the seeding was done in a similar manner, but the number of kernels varied somewhat because of the limited quantity of seed available from some of the F_2 selections. At Moccasin the 1924 sowings were not definitely spaced, but 2.3 grams of seed was used in each of the rows, which were 16 feet long and 1 foot apart. Checks of the parent varieties, sown in the same manner and at the same time as the F_3 hybrids, alternated in every tenth row at the three stations. The F_3 strains grown at Bozeman and Havre in 1924 were from F_2 plant selections from Bozeman in 1923. The F_3 strains grown at Moccasin in 1924 were from F_2 selections made at that station the previous year.

The material thus grown constitutes the basis for the following study. Probable errors for numbers of individuals where only two classes are concerned were obtained from tables of probable errors of Mendelian ratios prepared in the department of plant breeding of Cornell University, Ithaca, N. Y., from the formula $0.6744898 \sqrt{n\,p\,q}$, in which n is the total number of individuals and p and q the percentages corresponding to the ratios involved. Deviations from the expected which are less than three times their probable errors are not here considered significant.

When more than two classes are concerned, the goodness of fit to the expected ratio is determined by the X^2 method in which $X^2 = \Sigma \frac{(o-c)^2}{c}$. From X^2 the value of P is determined by interpolation from Elderton's table given by Pearson (*14*) for determining this value. The values of P usually are less than 1, which value represents a perfect fit. Ratios having deviations with a value of P lower than 0.043 are not here considered significant.

Correlations here reported were determined by the product moment coefficient of correlation method in which $r_{xy}=\frac{\Sigma_{xyf}}{n\sigma_x\sigma_y}\pm 0.6745\frac{1-r^2}{\sqrt{n}}$. Correlation coefficients greater than three times their probable errors are here considered statistically significant.

Plant selections were made in the F_2 and F_3 generations from their appearance in the field, their threshed grain, and from each frequency class for date of heading, date of ripening, fruiting period, height, yield, and crude-protein content. The dwarf plants introduced a possible difficulty in maintaining a random sample. The lack of evidence of linkage between dwarfness and other characters, together with the few instances of linkage ever recorded in wheat hybrids, minimizes the importance of this, and the writers feel that the normal plants, as selected, fairly represent a random sample.

SEGREGATION OF CHARACTERS IN THE F_2 AND F_3 GENERATIONS

The F_1 plants grown at Davis, Calif., in 1922 were all normal in stature, apically awnletted, brown glumed, and red kerneled. No further notes or comparative data with the parents were obtained in this generation.

A study of individual plants for the principal contrasting characters and factors for yield and quality was made on the F_2 material grown at Bozeman in 1923 and for some of the characters on similar material grown at Moccasin in the same year. The study was continued on F_3 material grown at Bozeman, Moccasin, and Havre in 1924, to determine the inheritance and the environmental effect on the material under the different representative Montana conditions.

The characters studied for their inheritance are dwarfness, awnedness, glume color, kernel color, curledness of leaves, heading period, ripening period, fruiting period, height, yield, and crude-protein content of the grain.

The reciprocal crosses were studied to determine the differential influence, if any, on the progeny. Dominance of the curled-leaf character appeared partially reversed in F_2 of reciprocal crosses. The studies made on this character will not be presented in this bulletin. The results of the studies of the other characters in the F_2 and F_3 generations follow in the order listed above.

DWARFNESS

Dwarf plants appeared in F_2 progenies of all F_1 families of the Marquis × Hard Federation and reciprocal wheat crosses grown at Bozeman and Moccasin in 1923. At Bozeman some of the dwarf plants headed at a height of about 6 inches and matured seed. At Moccasin, however, only a few produced heads late in the season, and none of them matured seed. The dwarf plants which did not head were similar to the grass clumps first described by Farrer (7). From the results at the two stations it appears probable that both genetic and environmental factors were in part responsible for differentiation into the groups hereafter called dwarfs and grass clumps.

At Bozeman there appeared in the F_2 progeny of six F_1 families 600 normal plants, 114 dwarfs, and 38 grass clumps; at Moccasin, in the F_2 progeny of six other F_1 families, there were 457 normals and 101

dwarfs and grass clumps, the two latter not being distinguishable. These results indicate that two genetic factors are involved, segregating in the F_2 progenies to give a 13 : 3 ratio for normals to combined dwarfs and grass clumps and in a 15 : 1 ratio for combined normals and dwarfs to grass clumps. As the Moccasin data do not permit the latter separation, the F_2 data from both stations are tabulated in only two classes—normals compared with dwarfs, the latter including grass clumps. The data for each of the F_1 families, the totals at each station, and the totals from both stations are given in Table 3.

TABLE 3.—*Segregation of 1,310 F_2 plants of the Marquis × Hard Federation wheats and reciprocal crosses into two classes, normal and dwarf plants, when grown at Bozeman and Moccasin, Mont., in 1923*

Source, cross, and hybrid No.	Number of F_1 families	F_2 plants			Deviation from 13 : 3 ratio	Probable error
		Normals	Dwarfs	Total		
BOZEMAN						
Marquis×Hard Federation:						
21202B1	1	96	27	123	4	2.92
21202B2	1	100	28	128	4	2.98
21202B3	1	101	26	127	2	2.97
Total:						
Number	3	297	81	378	10	5.12
Percentage		78.6	21.4			
Hard Federation×Marquis:						
21203A1	1	102	24	126	0	2.96
21203A2	1	101	27	128	3	2.98
21203A3	1	100	20	120	3	2.88
Total:						
Number	3	303	71	374	1	5.09
Percentage		81.0	19.0			
Grand total:						
Number	6	600	152	752	11	7.22
Percentage		79.8	20.2			
MOCCASIN						
Marquis×Hard Federation:						
21202A1	1	81	10	91	7	2.51
21202A2	1	72	22	94	4	2.55
21202A3	1	77	18	95	0	2.57
Total:						
Number	3	230	50	280	3	4.41
Percentage		82.1	17.9			
Hard Federation×Marquis:						
21203C1	1	81	15	96	3	2.58
21203C2	1	70	15	85	1	2.43
21203C3	1	76	21	97	3	2.59
Total:						
Number	3	227	51	278	1	4.39
Percentage		81.7	18.3			
Grand total:						
Number	6	457	101	558	4	6.22
Percentage		81.9	18.1			
Total (both stations):						
Number	12	1,057	253	1,310	7	9.53
Percentage		80.7	19.3			

The data show a close fit to the 13 : 3 ratio in each F_1 family and in their totals at both stations. The deviations in numbers in all cases are less than three times their probable errors. There is no

consistent or significant difference between reciprocal crosses, as the percentages alternate slightly at the two stations.

The study of normal and dwarf segregation was continued in the F_3 generation at Bozeman in 1924, where F_3 families were grown from 224 normal and 25 dwarf F_2 plants. The data obtained from normal plants are given in Table 4.

TABLE 4.—*Breeding behavior of 13,397 F_3 plants grown from seed of normal F_2 plants of crosses between Marquis and Hard Federation wheats, at Bozeman, Mont., in 1924*

Breeding behavior in the F_3 generation	Number of F_2 families	Expected on 7 : 4 : 2 ratio [1]	Percentage of—		Number of F_3 plants			Deviation from ratio indicated	Probable error	Corrected percentage of total F_2
			Normal plants	Stand	Normal	Dwarfs and grass clumps	Total			
Normals breeding true	127	121	56.7	85.2	7,570	----	7,570	----	----	45.3
Normals breeding 13 normals to 3 dwarfs	64	69	28.6	85.9	3,177	673	3,850	49	16.30	22.8
Normals breeding 3 normals to 1 dwarf	33	34	14.7	85.6	1,450	527	1,977	33	13.01	11.7
Total	224	224	100.0	85.4	12,197	1,200	13,397	----	----	79.8

[1] P=0.72.

The data show that of the thirteen-sixteenths which were normal plants in the F_2 generation, approximately seven parts bred true for normal plants and six parts segregated for normal and dwarfs in the F_3. The families throwing dwarfs were divided according to whether they were below or above 21.9 per cent for the 13:3 and 3:1 ratios accordingly. Of the six segregating parts, approximately four parts bred as in F_2 with 13 normals to 3 dwarfs, and two parts segregated in a 3:1 ratio of normals to dwarfs. A very close fit to the 7:4:2 ratio was obtained, P equaling 0.72. Of the four parts segregating in a 13:3 ratio, the deviation is greater than that in F_2. This is evidently due to the overlapping with the 3:1 ratio. The deviation of 49 ± 16.30, however, is no larger than would be expected by chance in 1 out of every 22 trials. The two parts segregating in a 3:1 ratio have a deviation of 33 ± 13.01, which is close to the expected ratio, as the deviation is but 2.5 times its probable error.

As shown, the percentage of stand for the three types was practically 85 per cent for each, so that it appears certain that the seed of the dwarfs is not less viable than those of the normals.

TABLE 5.—*Breeding behavior of 934 F_3 plants grown from dwarf F_2 plants of crosses between Marquis and Hard Federation wheats at Bozeman, Mont., in 1924*

Breeding behavior in the F_3 generation	Number of F_2 families	Percentage of—		Number of F_3 plants			Deviation from ratio indicated	Probable error	Corrected percentage of total F_2
		Dwarfs	F_2	Normal	Dwarfs	Total			
Dwarfs breeding 3 dwarfs to 1 normal	21	84.0	63.0	176	577	753	12	8.01	12.8
Dwarfs breeding true	4	16.0	12.0	----	181	181	----	----	2.4
Total	25	100.0	75.0	176	758	934	----	----	15.2

VARIETAL PLATS OF MARQUIS (*A*) AND HARD FEDERATION WHEAT (*B*), SHOWING DIFFERENCES IN HEIGHT AT BOZEMAN, MONT., IN 1924

INHERITANCE IN MARQUIS-HARD FEDERATION CROSSES

A, Typical spikes of the varieties used as parents in the cross, together with the first-generation progeny: *1*, Hard Federation; *2*, F_1 hybrid; *3*, Marquis. *B*, Spikes of F_2 hybrids representing the three classes for awnedness: *1*, Awnless; *2*, apically awnletted; *3*, awnletted

Of the 152 dwarf F_2 plants grown at Bozeman in 1923, 114, or 75 per cent, matured seed and 38, or 25 per cent, did not head and produce seed and were classed as grass clumps. Of the first class 25 were grown at Bozeman in 1924. The breeding behavior of these strains in the F_3 generation is shown in Table 5.

Of the 25 F_2 dwarf strains 4, or 16 per cent, bred true for dwarfness, and the remainder segregated in a ratio not significantly different from 3 dwarfs to 1 normal. Assuming that 16 per cent of the 114 dwarfs in the F_2 population would have proved homozygous if tested, it appears that there were about 18 fertile homozygotes to be added to the 38 sterile grass clumps, making 56 in all. Correcting the F_2 Bozeman results on a percentage basis of F_3 plants grown at that station, the figures shown in Table 6 are obtained.

TABLE 6.—*Correction of the Bozeman F_2 dwarf data on the basis of F_3 results*

Descriptive items	Dwarfs	Grass clumps
Obtained (uncorrected) in F_2	114	38
Corrected on basis of F_3	96	56
Calculated on 2 : 1 ratio	101	51
Deviation	5	5
Probable error	3.92	

This corrected deviation of 5 ± 3.92 is a close fit to the expected 2 : 1 ratio, as it is within three times the probable error. It is important to note that at Bozeman in 1924 the four true-breeding F_2 dwarf families all headed and matured seed. From these data it seems that the grass clumps appear only as a homozygous condition of dwarfness, the ability of the plants to head and mature seed being due to environmental conditions.

An interpretation of the above data can be satisfactorily made on a genetic basis by assuming DD a factor for dwarfs and NN an inhibitor or factor for normals. As Waldron (*20*) has shown, Kota × Marquis hybrids produce dwarfs in ratios involving two or three genetic factors, and Clark (*5*) observed no dwarfs in Kota × Hard Federation crosses, the formula for Marquis could be DDNN and Hard Federation ddnn, or vice versa. A dominant third factor necessary for dwarfness may be present in Marquis and Hard Federation but lacking in Kota. As this would be common to the varieties dealt with here, it need not be represented in the formulas. The F_1 of the Marquis × Hard Federation cross will thus be represented as DdNn. The following formulas may represent the F_2 genotypes and their breeding behavior in the F_3 generation:

1 DDNN	Normals, breeding true to normals.
2 DdNN	
1 ddNN	
2 ddNn	
1 ddnn	
7	
4 DdNn	Normals breeding 13 normals to 3 dwarfs.
2 DDNn	Normals, breeding 3 normals to 1 dwarf.
2 Ddnn	Dwarfs, breeding 3 dwarfs to 1 normal.
1 DDnn	Dwarfs, breeding true to dwarfs.

The corrected numbers corresponding to this 7 : 4 : 2 : 2 : 1 genotypic ratio from the Bozeman F_2 data of 752 plants are 340 : 172 : 88 : 96 : 56. The calculated on the above ratio would be 329 : 188 : 94 : 94 : 47. The deviations in each class are 11, 16, 6, 2, 9, from which the value of 0.42 for P indicates a very close fit.

AWNEDNESS

Biffen (*2*) was first to point out that the awnless condition of a wheat spike is dominant. Other early workers obtained similar results in the first generation and also found that in the second generation awnless and awned plants occur in the single Mendelian ratio of 3 : 1 or of 1 : 2 : 1 when intermediates occur. Howard and Howard (*11*) were the first to record two factors in the inheritance of awns when they grouped all awned and awn-tipped classes as awned, which in comparison with awnless gave a 15 : 1 ratio. They thus concluded the awned condition to be dominant.

Clark (*5*) has shown that in Kota–Hard Federation crosses two genetic factors did not entirely account for the breeding behavior in F_2 and F_3 after the material was classified into five classes; that is, (1) awnless, as Hard Federation; (2) apically awnletted; (3) awnletted; (4) short awned; and (5) awned, as Kota. The F_1 represented class 2, apically awnletted, and in F_3 all F_2 classes segregated into at least four classes. Two genetic factors would explain the behavior of strains breeding true for classes 1 and 2 and also those for classes 4 and 5, but an additional factor or factors would be necessary to account for the variation remaining.

In the present study (pl. 2), in which Hard Federation is awnless (class 1+), Marquis is awnletted (class 3−), and F_1 apically awnletted (class 2), the F_2 and F_3 material is separable into three classes, (1) awnless, (2) apically awnletted, and (3) awnletted. Class 1, awnless, usually is without awnlets in the apical portion of the spike, although, like Hard Federation (1+), it sometimes has a few awnlets 1 to 2 millimeters long. Class 2, apically awnletted, has awnlets 2 to 20 millimeters long at the apex of the spike, but rarely extending to the central and basal portions. Class 3, awnletted, has awnlets from 3 to 40 millimeters long, the shorter occurring at the base of the spike and the length increasing toward the apex, where many exceed the length of the awnlets on Marquis (3−) by 10 to 20 millimeters. It is seen from Plate 2, *A* and *B*, that selections of the hybrid have a greater awn development than Marquis.

The data by classes, obtained in F_2 at Bozeman and Moccasin in 1923, are given in Table 7. Only normal plants are included in this study.

The data given in Table 7 show segregation into the three awnedness classes for 12 F_1 families, of which 6 were grown at Bozeman and 6 at Moccasin and of which 3 represent reciprocal crosses at each station. The results from reciprocal crosses at the two stations do not show significant differences. At Bozeman the Hard Federation × Marquis families in which the awnless Hard Federation parent was the female, have a slightly higher percentage of awnless plants, and the Marquis × Hard Federation families in which the awnletted Marquis parent was the female, have a slightly larger percentage of awnletted plants. At Moccasin the same relationship existed for the

awnless segregates, but there were much larger percentages of awnletted plants in the Hard Federation × Marquis crosses than in the reciprocal. There is no consistent or significant evidence, therefore, of maternal influence affecting the awnedness factors in reciprocal crosses of these wheats.

TABLE 7.—*Segregation in the F_2 generation into three classes for awnedness of 1,050 plants of 12 Marquis × Hard Federation wheats and reciprocal crosses grown at Bozeman and Moccasin, Mont., in 1923*

Station, cross, and hybrid No.	Number of F_1 families	F_2 plants by awnedness classes				1 : 15 ratio for class 1 to classes 2 and 3		3 : 1 ratio for classes 1 and 2 to class 3	
		1, awnless	2, apically awnletted	3, awnletted	Total	Deviation	Probable error	Deviation	Probable error
BOZEMAN									
Marquis×Hard Federation:									
21202B1	1	7	70	21	98	1	1.62	4	2.89
21202B2	1	6	71	21	98	0	--------	4	2.89
21202B3	1	4	71	25	100	2	1.63	0	--------
Total:									
Number	3	17	212	67	296	2	2.81	7	5.02
Percentage	--------	5.8	71.6	22.6	100	--------	--------	--------	--------
Hard Federation×Marquis:									
21203A1	1	9	71	16	96	3	1.60	8	2.86
21203A2	1	7	77	13	97	1	1.61	11	2.88
21203A3	1	5	83	12	100	1	1.63	13	2.92
Total:									
Number	3	21	231	41	293	3	2.79	32	5.00
Percentage	--------	7.2	78.8	14.0	100	--------	--------	--------	--------
Grand total:									
Number	6	38	443	108	589	1	3.96	39	7.09
Percentage	--------	6.5	75.2	18.3	100	--------	--------	--------	--------
MOCCASIN									
Marquis×Hard Federation:									
21202A1	1	7	57	17	81	2	1.47	3	2.63
21202A2	1	3	54	15	72	2	1.39	3	2.48
21202A3	1	2	49	26	77	3	1.43	7	2.56
Total:									
Number	3	12	160	58	230	2	2.48	0	--------
Percentage	--------	5.2	69.6	25.2	100	--------	--------	--------	--------
Hard Federation×Marquis:									
21203C1	1	6	51	24	81	1	1.47	4	2.63
21203C2	1	3	48	22	73	2	1.39	4	2.50
21203C3	1	7	51	19	77	2	1.43	0	--------
Total:									
Number	3	16	150	65	231	2	2.48	7	4.44
Percentage	--------	6.9	65.0	28.1	100	--------	--------	--------	--------
Grand total:									
Number	6	28	310	123	461	1	3.51	8	6.27
Percentage	--------	6.1	67.2	26.7	100	--------	--------	--------	--------
Total (both stations):									
Number	12	66	753	231	1,050	0	--------	32	9.47
Percentage	--------	6.3	71.7	22.0	100	--------	--------	--------	--------

Combining classes 1 and 2 and comparing with class 3, the data are shown to be close to a 3 : 1 ratio except for two F_1 families at Bozeman. By combining classes 2 and 3 in comparison with 1, the data from 12 families at two stations are close to a 15 : 1 ratio. These data indicate the presence of one and two genetic factor differences.

The segregation of the Bozeman material into the three classes conformed closely to a 1:12:3 ratio, and that of the Moccasin material was near a 1:11:4 ratio. It was therefore necessary to make a careful study of the F_3 material to determine the breeding behavior of the different classes. This study was made at Bozeman in 1924 on material grown from F_2 Bozeman seed. The behavior of the three classes in the F_3 generation is presented in Table 8.

TABLE 8.—*Breeding behavior in the F_3 generation of 12,197 plants from Marquis–Hard Federation wheat crosses of the three awnedness classes grown at Bozeman, Mont., in 1924*

F_2 classes and their breeding behavior in the F_3 generation	F_2 families		Number of F_3 plants by awnedness classes				Corrected percentage of F_2
	Number	Percentage of class	1, awnless	2, apically awnletted	3, awnletted	Total	
1, awnless:							
1	26	83.9	1,382			1,382	5.41
1 and 2	4	12.9	62	177		239	.83
1, 2, and 3	1	3.2	4	30	14	48	.21
Total	31	100.0	1,448	207	14	1,669	6.45
2, apically awnletted:							
1	1	.7	46			46	.51
2	17	11.3		946		946	8.52
1 and 2	23	15.3	278	900		1,178	11.53
1, 2, and 3	44	29.3	185	1,683	636	2,504	22.06
2 and 3	56	37.3		1,699	1,271	2,970	28.08
3	9	6.0			476	476	4.51
Total	150	99.9	509	5,228	2,383	8,120	75.21
3, awnletted:							
3	43	100.0			2,408	2,408	18.34
Grand total	224	300.0	1,957	5,435	4,805	12,197	100.00

To interpret the data on a one-factor basis there must necessarily be approximately 25 per cent of true-breeding recessives. These recessives may be among those plants having either more or less awn development than the F_1, which was apically awnletted (class 2) and intermediate between the two parents.

In the F_2 generation, combining classes 1 and 2, the plants as classified gave the percentages shown in Table 9.

TABLE 9.—*Percentage totals of F_2 results by combining classes 1 and 2 in comparison with class 3*

Localities	Classes 1 and 2	Class 3
Bozeman	81.7	18.3
Moccasin	73.3	26.7
Percentage of total	78.0	22.0

The awnletted class 3 from Bozeman material bred true in the F_3 generation, and as shown in Table 8 nine families also bred true for class 3 that had been described in F_2 as belonging to class 2.

The breeding behavior of the F_2 classes in the F_3 generation by percentages in comparison with the calculated was as shown in Table 10.

TABLE 10.—*Comparison of the breeding behavior of the two classes with that calculated*

Comparative items	F_2 families	F_3 plants	
		Classes 1 and 2	Class 3
Obtained	26.8	100.0	
	50.3	65.2	34.8
	22.9		100.0
Calculated	25.0	100.0	
	50.0	75.0	25.0
	25.0		100.0

A fairly close fit to the expected 1:2:1 ratio was obtained for the F_2 families involved. There resulted, however, an excess of class 3 plants in the F_3 generation.

On the basis of the F_3 distribution, assuming that 22.9 per cent of the Bozeman F_2 families would have proved homozygous for class 3 if tested, it appears that 4.51 per cent should be added to the 18.34 per cent, as originally classified. Correcting the Bozeman F_2 data on the F_3 results, the figures obtained agree closely with the original Moccasin data. (Table 11.)

TABLE 11.—*Comparison of the corrected Bozeman and original Moccasin data*

Station	Classes 1 and 2	Class 3	Deviation from 3:1 ratio	Probable error
Bozeman (corrected)	454	135	12	7.09
Moccasin (original)	338	123	8	6.27
Total (both stations)	792	258	5	9.47

These deviations are less than three times their probable errors and show a fit which is not significantly different from the one factor or 3:1 ratio. It seems reasonably certain, therefore, that there is a primary factor for the degree of awn development of Marquis (class 3) which is recessive to a factor determining less awn development.

On the hypothesis that a second factor is responsible for the differences between the awnless and apically awnletted classes, it will be necessary to find 6.25 per cent of recessives of F_2 strains at the other extreme breeding true.

TABLE 12.—*Percentage totals of F_2 results obtained by combining classes 2 and 3 in comparison with class 1*

Localities	Class 1	Classes 2 and 3
Bozeman	6.5	93.5
Moccasin	6.1	93.9
Percentage of total	6.3	93.7

The F_2 plants as classified fell into groups with percentage values as shown in Table 12.

In the F_3 generation the Bozeman material bred into percentage distributions in comparison with the calculated as shown in Table 13.

TABLE 13.—*Comparison of the breeding behavior of the two classes with that calculated*

Comparative items	F_2 families	F_3 plants	
		Class 1	Classes 2 and 3
Obtained	5.92	100.0	
	12.36	24.6	75.4
	22.27	7.4	92.6
	59.45		100.0
Calculated	6.25	100.0	
	25.00	25.0	75.0
	25.00	6.25	93.75
	43.75		100.00

A close fit was obtained for the percentage distribution of F_3 plants. There was, however, an excess of F_2 families breeding true for the combined 2 and 3 classes and a deficiency in the second group breeding in a 1:3 ratio. Correcting the Bozeman F_2 data on the F_3 results, the figures shown in Table 14 are obtained for the total F_2.

TABLE 14.—*Comparison of the corrected Bozeman and original Moccasin data*

Station	Class 1	Classes 2 and 3	Deviation from 1:15 ratio	Probable error
Bozeman (corrected)	35	554	2	3.96
Moccasin (original)	28	433	1	3.51
Total (both stations)	63	987	3	5.28

The deviations are less than three times their probable errors and show a fit which is not significantly different from a 2-factor or 1:15 ratio.

The classification of F_2 material resulted in a shortage of plants in class 3, while there was an excess of plants of this class in F_3. It is apparent that environment affects the awnedness of plants differently in different seasons and that the results of classification did not exactly coincide in either year with the genetic constitution of the hybrid plants. In general, however, the results indicate the presence of two pairs of factors.

TABLE 15.—*Correction of the Bozeman F_2 awnedness data for the three classes on the basis of the F_3 results*

Descriptive items	Class 1	Class 2	Class 3	Deviations	Value of *P.*
Bozeman:					
Original	38	443	108	1, 38, 39	0.001
Corrected on F_3	35	419	135	2, 14, 12	.446
Calculated on 1:11:4 ratio	37	405	147		

The expected ratio for the three awnedness classes on the above hypothesis is 1:11: 4. It will be recalled that the distribution of the original Moccasin F_2 data was close to this ratio, but that of the Bozeman data was nearer a 1:12:3 ratio. Correcting the Bozeman F_2 data for the three classes on the Bozeman F_3 results, the figures shown in Table 15 are obtained.

A close fit to the expected ratio for the corrected Bozeman data is thus obtained.

A genetic interpretation of these results can best be made by assuming that a primary factor pair (A, a) is responsible for the distinction between the awnlessness or short awn development of classes 1 and 2 (dominant) as opposed to the longer awn development of class 3 (recessive). Complete dominance is not indicated, as it is postulated that it requires the homozygous "dominant" (AA) combined with the recessive bb of a secondary pair of factors to give complete elimination of awns (class 1).

The formula for Hard Federation (1) would be AAbb, Marquis (3) aaBB, and the F_1 AaBb. In the F_2 generation the following formulas may represent the breeding behavior of the three classes in F_3:

Class 1:	
1 AAbb	Awnless; breeding true.
Class 2:	
4 AaBb	Apically awnletted; segregating as F_2 in 1:11:4 ratio.
2 AABb	Apically awnletted; segregating for 1 awnless to 3 apically awnletted.
2 AaBB	Apically awnletted; segregating for 3 apically awnletted to 1 awnletted.
2 Aabb	Apically awnletted; segregating for 1 awnless to 2 apically awnletted to 1 awnletted.
1 AABB	Apically awnletted; breeding true.
11	
Class 3:	
2 aaBb	Awnletted; breeding true.
1 aaBB	Awnletted; breeding true.
1 aabb	Awnletted; breeding true.
4	

The awnletted allelomorph in the primary pair (Aa) of factors is represented as recessive in accord with its primary effect. On the other hand, it is the awnlessness factor of the second pair (Bb) that is represented as recessive in accordance with the one effect ascribed to it in this cross.

Of 145 F_2 families of class 2, one-eleventh, or 13 families, would be expected to breed true. It is shown in Table 8 that 17 families were of that sort. The segregation of the remaining class 2 groups can be determined accurately only by correcting F_3 data on the basis of F_4 results, which has not yet been done.

From the F_3 data, however, which prove classes 1 and 3 are true breeding and that the expected portion of class 2 also breeds true, it appears probable that the 1 : 11 : 4 ratio is the essential explanation of inheritance of awnedness in the three awnedness classes in this cross. The corrected numbers corresponding to this 1 : 11 : 4 ratio from the Bozeman data of 1,050 F_2 plants are 63, 729, and 258

plants, respectively. The expected numbers are 66, 722, and 262. The deviations are 3, 7, 4, and the value of P, 0.896 indicates a very close fit.

GLUME COLOR

Glume colors of wheat are most commonly classed as white and brown. Biffen (*2*) was first to report brown glume color dominant over white in the single 3 : 1 ratio. No other ratio is known to have been found in crosses between varieties of common wheats.

The present study includes data on the segregation of F_2 plants for color of glumes at Bozeman and Moccasin in 1923. The results obtained are shown in Table 16.

TABLE 16.—*Segregation in the F_2 generation into brown and white glume classes of 1,050 plants of Marquis–Hard Federation wheats and reciprocal crosses grown at Bozeman and Moccasin, Mont., in 1923*

Station, cross, and hybrid No.	Number of F_1 families	F_2 plants by glume color			Deviation from 3 : 1 ratio	Probable error
		Brown	White	Total		
BOZEMAN						
Marquis×Hard Federation:						
21202B1	1	77	21	98	4	2.89
21202B2	1	68	30	98	5	2.89
21202B3	1	71	29	100	4	2.92
Total:						
Number	3	216	80	296	6	5.02
Percentage		73.0	27.0			
Hard Federation×Marquis:						
21203A1	1	73	23	96	1	2.86
21203A2	1	74	23	97	1	2.88
21203A3	1	77	23	100	2	2.92
Total:						
Number	3	224	69	293	4	5.00
Percentage		76.5	23.5			
Grand total:						
Number	6	440	149	589	2	7.09
Percentage		74.7	25.3			
MOCCASIN						
Marquis×Hard Federation:						
21202A1	1	54	27	81	7	2.63
21202A2	1	55	17	72	1	2.48
21202A3	1	58	19	77	0	2.56
Total:						
Number	3	167	63	230	5	4.43
Percentage		72.6	27.4			
Hard Federation×Marquis:						
21203C1	1	59	22	81	2	2.63
21203C2	1	61	12	73	6	2.50
21203C3	1	59	18	77	1	2.56
Total:						
Number	3	179	52	231	6	4.44
Percentage		77.5	22.5			
Grand total:						
Number	6	346	115	461	0	
Percentage		75.1	24.9			
Total (both stations):						
Number	12	786	264	1,050	1	9.47
Percentage		74.9	25.1			

There is no evidence of maternal influence in the reciprocal crosses, although there are small consistent differences in the percentages at the two points. The percentages of brown-glumed plants are slightly greater when Hard Federation is used as the female parent and the percentages of white-glumed plants slightly greater with Marquis as the female parent. In all cases, however, the differences are not sufficiently large to be significant.

The deviations in numbers from the simple 3:1 ratio are not significantly different in any family or in the several totals. In general, the F_2 data show a remarkably close fit. The study was continued on the F_3 generation at Bozeman, and the data obtained are given in Table 17.

TABLE 17.—*Breeding behavior in the F_3 generation of white and brown glume classes and 12,197 plants of Marquis–Hard Federation wheat crosses grown at Bozeman, Mont., in 1924*

F_2 classes and their breeding behavior in the F_3 generation	F_2 families		Number of F_3 plants by glume color			Deviation from 3:1 ratio	Probable error
	Number	Expected on 2:1 ratio	Brown	White	Total		
Glumes white:							
White	51	----------	----------	2,840	2,840	----------	----------
Glumes brown:							
Brown and white	108	115	4,357	1,438	5,795	11	22.19
Brown	65	58	3,562	----------	3,562	----------	----------
Total	224	----------	7,919	4,278	12,197	----------	----------

These data show that the white-glumed plants all bred true and that the brown-glumed plants either bred true or segregated in a 3:1 ratio in proportions which approximate the ratio of 2:1.

KERNEL COLOR

The inheritance of red kernel color was first reported by Biffen (*2*) to be dominant over white in F_1 and to segregate in a 3:1 ratio in F_2. Nilsson-Ehle (*13*) first reported crosses which in F_2 gave 15:1 and 63:1 ratios of red-kerneled to white-kerneled plants, proving the presence of two and three genetic factors. Similar ratios have been found since by other workers.

In the present study red proved dominant as usual in the F_1 generation. The data on segregation of F_2 plants from 12 F_1 families including reciprocal crosses are given in Table 18.

The data in Table 18 show little or no difference between reciprocal crosses. Of the 12 families 10 show a close fit to a 2-factor or 15:1 ratio and the remaining two families, 2A1 and 2A3, to a 1-factor or 3:1 ratio. The deviation in numbers, for each family and for the totals, are all less than three times their probable errors. The fact that two different ratios were obtained indicates that either Marquis does not have homozygous dominant factors for kernel color or shows that the Hard Federation male-parent plants differed in their genotype. Family 2A2 which segregated in a 15:1 ratio was produced from an F_0 kernel produced on the same spike

as those from which families A1 and A3 descended. The pollen, however, was collected at random from several plants in a row of Hard Federation.

TABLE 18.—*Segregation in the F_2 generation into red and white kernel classes of 1,052 plants of Marquis–Hard Federation and reciprocal wheat crosses grown at Bozeman and Moccasin, Mont., in 1923*

Station, cross, and hybrid No.	Number of F_1 families	F_2 plants by kernel color			Deviation from 15:1 ratio	Probable error
		Red	White	Total		
BOZEMAN						
Marquis×Hard Federation:						
21202B1	1	91	8	99	2	1.62
21202B2	1	94	4	98	2	1.62
21202B3	1	92	8	100	2	1.63
Total:						
Number	3	277	20	297	2	2.81
Percentage		93.3	6.7			
Hard Federation×Marquis:						
21203A1	1	93	3	96	3	1.60
21203A2	1	95	3	98	3	1.62
21203A3	1	94	6	100	0	1.63
Total:						
Number	3	282	12	294	6	2.80
Percentage		95.9	4.1			
Grand total:						
Number	6	559	32	591	5	3.97
Percentage		94.6	5.4			
MOCCASIN						
Marquis×Hard Federation:						
21202A1	1	64	17	81	[1] 3	2.63
21202A2	1	66	6	72	1	1.39
21202A3	1	63	14	77	[1] 5	2.56
Total:						
Number	1	66	6	72	1	1.39
Percentage		91.7	8.3			
Hard Federation×Marquis:						
21203C1	1	74	7	81	2	1.47
21203C2	1	69	4	73	1	1.39
21203C3	1	69	8	77	3	1.43
Total:						
Number	3	212	19	231	5	2.48
Percentage		91.8	8.2			
Grand total:						
Number	4	278	25	303	6	2.84
Percentage		91.7	8.3			
Total (both stations):						
Number	10	837	57	894	1	4.88
Percentage		93.6	6.4			

[1] Deviation from 3:1 ratio.

The study was continued in F_3 material from Bozeman, all of which in F_2 segregated in a 15:1 ratio. The data obtained are given in Table 19.

The material at Bozeman in 1924 was affected by root-rot to the extent of about 18 per cent. The plants affected matured prematurely and produced kernels very much shrunken. For this reason no accurate classification of the affected plants could be made for kernel color, and only plants having normal kernels were included

in this F_3 study. The number of plants recorded, therefore, is less than in the case of the characters previously studied.

TABLE 19.—*Breeding behavior in the F_3 generation of white and red kernel classes and 10,121 plants of Marquis–Hard Federation wheat crosses grown at Bozeman, Mont., in 1924*

F_2 classes and breeding behavior in the F_3 generation	F_2 families		Number of F_3 plants by kernel color			Deviation from ratio indicated	Probable error
	Number	Expected on 7:4:4 ratio[1]	Red	White	Total		
Kernels white:							
White	16			763	763		
Kernels red:							
Red	101	97	4,476		4,476		
Red and white—							
3:1 ratio	43	56	1,485	458	1,943	28	12.87
15:1 ratio	64	55	2,734	205	2,939	21	8.84
Total	224		8,695	1,426	10,121		

[1] P=0.10.

The data given in Table 19 show that the white-kerneled strains bred true and that the red ones either bred true or segregated in a 3:1 or 15:1 ratio, in proportions approximating a 7:4:4 ratio. There was a slight excess of true-breeding red-kerneled F_2 families, and also the number of families having two factors or breeding in a 15:1 ratio was somewhat larger than expected on a 7:4:4 ratio. This excess may be due to the selection of a part of the material for dark-red color. This also might have caused a shortage in the number of families segregating in the 3:1 ratio. The deviations in numbers of both segregating groups are less than three times their probable errors, thus indicating a close fit.

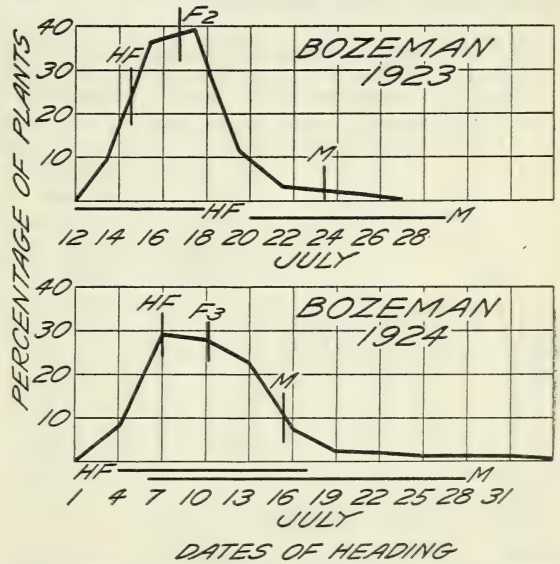

FIG. 1.—Frequency distribution of F_2 and F_3 hybrid wheat plants and the range of variation of the Marquis and Hard Federation parents, together with their average dates of heading at Bozeman, Mont., in 1923 and 1924

HEADING PERIOD

Early maturity usually has been considered one of the important factors for improvement in varietal adaptation under droughty conditions. Under favorable conditions, however, earliness seldom is considered an advantage and when obtained usually results in a

sacrifice of yield. The importance of a study of the effect of maturity under the three different Montana conditions is apparent. This study has been made from the dates of heading, dates of ripening, and the days between these dates or from the heading, ripening, and fruiting periods.

The heading period usually is least affected by environmental conditions, and the senior writer (*5*) has thought that it is the best measure to use in a study of maturity inheritance.

Farrer (*7*) found that the heading period in F_1 hybrids is intermediate to those of the parents and that there was no difference in this respect in reciprocal crosses. Bryan and Pressley (*3*), in crosses between Sonora and Turkey, found the F_1 intermediate in time of heading to the parents and the F_2 majority inclined toward the late parent. Clark (*5*) in Kota×Hard Federation and reciprocal crosses found in F_2 studies at three points that earliness, as determined by date of heading, is dominant to lateness and that there were slight but significant differences in reciprocal crosses. Florell (*9*), from F_2 results with Sunset-Marquis crosses, also concluded that early heading is dominant and found that "there was a distinct heaping up of the population into a large early and a small late group in the proportion of 3.07 to 0.93."

In the present study, comparisons of dates of heading of the F_1 generation with parents are not available, but F_2 data from reciprocal crosses grown at Bozeman in 1923 with those from parent plants are presented in Table 20 and are shown graphically in Figure 1. All dwarf plants were omitted from this study. The dates of heading were obtained by tagging the plants individually on the day the first head emerged from the sheath.

TABLE 20.—*Segregation in the F_2 generation into daily frequency classes for date of heading of 583 plants of Marquis×Hard Federation and reciprocal wheat crosses, in comparison with the parents, grown at Bozeman, Mont., in 1923*

Dates of heading	Number of plants				
	F_2 hybrid			Hard Federation	Marquis
	Hard Federation×Marquis	Marquis×Hard Federation	Total		
July 12				9	
July 13	10	2	12	18	
July 14	33	13	46	38	
July 15	63	35	98	8	
July 16	64	45	109	23	
July 17	61	76	137	1	
July 18	31	60	91	2	
July 19	8	37	45		
July 20	9	12	21		1
July 21	3	9	12		11
July 22	2	1	3		19
July 23	3	2	5		26
July 24	2		2		13
July 25		1	1		19
July 26		1	1		4
July 27					4
July 28					1
July 29					2
Total	289	294	583	99	100
Mean and probable error[1]	16.30±0.08	17.27±0.07	16.79±0.05	14.29±0.09	23.52±0.12

[1] It is recognized that a date is a unit, but for averages it seems necessary to use fractional dates in order to show accurate differences in time of heading and ripening.

The data do not show large early and small late groups but indicate that early heading is partially dominant, as the mean date of heading of the hybrids was nearer that of the early Hard Federation parent. The reciprocal crosses show slight maternal influence, with a difference of 0.97 ± 0.11 days in mean date of heading. Statistically this difference, which is 8.8 times its probable error, is significant, as is also the difference of the mean of each reciprocal cross from the mean of the total F_2 population.

The variability of the hybrids is much greater than that of either of the parents. The extreme dates for earliness or lateness in both parents, however, were not reached by any of the F_2 plants. Variability constants, determined by computing the vegetative period, or days from emergence to heading, for the parents and the hybrid material are given in Table 21.

TABLE 21.—*Mean, standard deviation, and coefficient of variation for the vegetative period, or days from emergence to heading, of F_2 hybrids and for the Hard Federation and Marquis parents grown at Bozeman, Mont., in 1923*

Material compared	Mean (days)	Standard deviation	Coefficient of variation
F_2 hybrid	45.79±0.05	1.956±0.039	4.272±0.084
Hard Federation	43.29± .09	1.373± .066	3.172± .152
Marquis	51.52± .12	1.819± .087	3.531± .168

The data show that the F_2 hybrids are much more variable than either parent. The differences in the coefficient of variation of the F_2 hybrids and that of Marquis, the most variable parent, is 0.741 ± 0.188, which difference, being 3.9 times its probable error, indicates odds of over 116 to 1 that the occurrence of such variation was not due to chance alone.

TABLE 22.—*Dates of first heading in the F_3 generation of 674 Marquis–Hard Federation wheat hybrids, in comparison with 79 parent checks, grown in nursery rows at Bozeman, Moccasin, and Havre, Mont., in 1924*

Dates of first heading	Number of rows								
	Bozeman			Moccasin			Havre		
	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Hard Federation	Marquis
July 2				2	4				
July 3	2	5		9	5				
July 4	39	7		22					
July 5	66	1		26					
July 6	56			28			5		
July 7	39		2	37			15	8	
July 8	17		3	24			40	10	
July 9	3		1	2		5	74		
July 10	1		7			4	102		
July 11	1						28		
July 12							23		6
July 13							11		10
July 14							2		1
Total	224	13	13	150	9	9	300	18	17
Average date, July	5.7	3.7	9.0	5.9	2.6	9.4	9.7	7.6	12.7

In 1924 at Bozeman, Moccasin, and Havre F_3 strains were grown in nursery rows with one or the other of the two parents as a check every tenth row. Three notes were taken on dates of heading at each point: (1) First heading, (2) 50 per cent headed, and (3) fully headed. A careful study of all these data indicates that first heading is the most definite and therefore the most valuable of the three notes. The frequency data obtained on first heading are shown for the three stations in Table 22 and graphically in Figure 2.

The data in Table 22 give further evidence that early heading is partially dominant, the mean date of first heading of the hybrids at the three stations averaging 2.5 days later than the early parent and

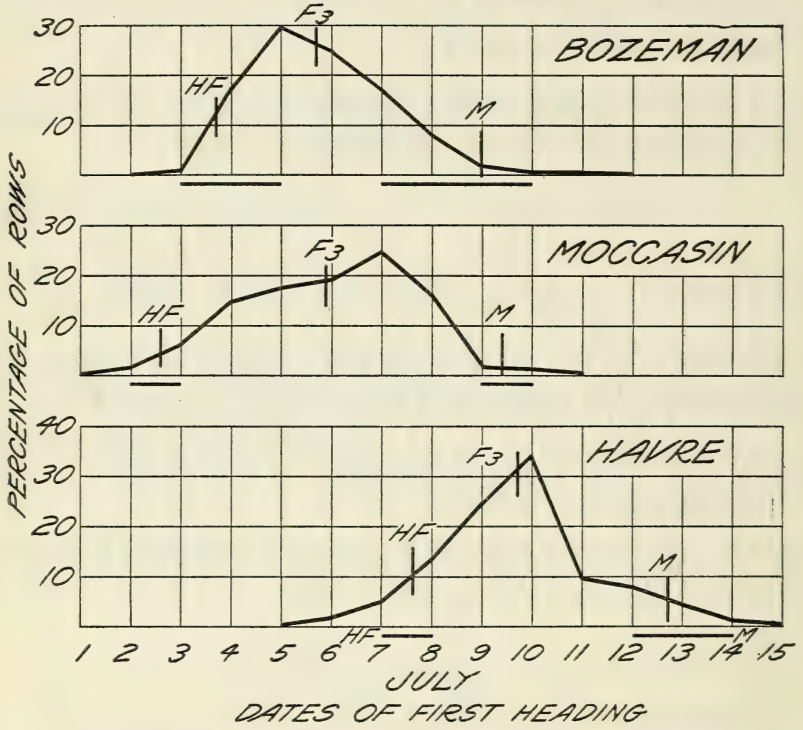

FIG. 2.—Frequency distribution of F_3 hybrid wheat strains and the range of variation of the Marquis and Hard Federation parents, together with their average dates of first heading at Bozeman, Moccasin, and Havre, Mont., in 1924

3.3 days earlier than the later parent. The F_3 data for date of first heading on a row basis show greater variability for the F_3 hybrids in comparison with the parents than did those for date of heading of individual F_2 plants.

At Bozeman 25 F_3 strains and at Havre 16 of the same strains were studied in 1924 on an individual-plant basis by labeling the F_3 plants for date of heading. Duplicate rows of each of the parent varieties were studied in a similar manner. There were some marked variations among the frequency distributions of the various F_3 strains, in that some approximated smooth curves and others bimodal curves. Strain A3–90 in Table 23 is an example of a bimodal curve.

This indicates that at least two genetic factors are involved for early heading in this cross and that in the F_3 generation some F_2 families appear to be segregating in a simple 3 : 1 ratio, as found by Florell (*9*).

Some of the earliest and latest heading F_2 plants were included among the families studied on an individual-plant basis, in order to determine their breeding behavior in F_3. It was desired to determine whether transgressive segregation occurred for date of heading. Data for the two earliest studied strains compared with the nearest studied check row of Hard Federation and for the two latest studied F_3 strains compared with the nearest studied check row of Marquis at each of the two stations are given in Table 23.

TABLE 23.—*Dates of heading of individual* F_3 *plants from early and late strains of Marquis–Hard Federation crosses, in comparison with the parents, grown at Bozeman and Havre, Mont., in 1924*

Dates of heading	Bozeman strain and row numbers						Havre strain and row numbers					
	Early heading			Late heading			Early heading			Late heading		
	A3–90; 223	A3–92; 224	Hard Federation; 220	A2–77; 17	B1–78; 4	Marquis; 10	B3–84; 222	A3–92; 139	Hard Federation; 40	A2–77; 72	B1–78; 26	Marquis; 10
Aug. 4			8									
Aug. 5	4	3	22									
Aug. 6	24	12	22	1		1						
Aug. 7	11	15	3			2			1			
Aug. 8	5	6				1			8			
Aug. 9	4	1	6		1	3	1		15			
Aug. 10		3			1	4	5	12	21			
Aug. 11	1	5	2	4	2	2	5	7	13			
Aug. 12	6	2		3	5	1	4	7	4			
Aug. 13	4	3	1	5	1	7	15	2	1	2	1	9
Aug. 14	1			6	12	12	6	5	1	8	1	27
Aug. 15		2		5	6	7	4			9		10
Aug. 16				6	7	10	1	1		4		7
Aug. 17				4	4	3				4	3	3
Aug. 18					1	2	1			4	1	1
Aug. 19				1	1	1				3	2	2
Aug. 20				5		2					2	1
Aug. 21				3	1	2				1		1
Aug. 22				3	4	1					5	
Aug. 23											1	1
Aug. 24				2	1							
Aug. 25					1	1						
Aug. 26				1	3							
Aug. 27					1							
Aug. 28					1							
Total	60	52	64	49	53	62	42	34	64	35	16	62
Average date, Aug.	7.8	8.2	6.0	16.2	16.6	14.3	12.7	11.6	9.9	15.9	19.2	15.0

The three early F_3 strains A3–90, A3–92, and B3–84 are the progeny of F_2 plants which headed on July 13, 14, and 16, 1923. The average date of heading of Hard Federation in 1923 was July 14. In the F_3 generation none of these strains was earlier than Hard Federation in average date of heading.

Of the late F_3 strains studied, the F_2 plant, of which family B1–78 was the progeny, was later than all others and headed on July 26, while the F_2 generation of strain A2–77 headed on July 23, 1923. The average date of heading for the late Marquis parent was July 24, 1923. In the F_3 generation both of these strains headed significantly later than the nearest studied Marquis check row at both

Bozeman and Havre. The means and differences, with their probable errors, are shown in Table 24.

As the differences are all greater than three times their probable errors, it appears that transgressive segregation for lateness of heading has been obtained.

TABLE 24.—*Comparison of two late-heading strains with nearest Marquis checks*

Strains compared	Bozeman	Havre
B1–78	16.6±0.43	19.2±0.53
Marquis	14.3± .32	15.0± .17
Difference	2.3± .54	4.2± .56
A2–77	16.2± .39	15.9± .22
Marquis	14.3± .32	15.0± .17
Difference	1.9± .50	.9± .28

One of the most striking features of the individual F_3 plant data is the variation in the number of days required for the different strains to pass through the heading stage from first heading to fully headed. Florell (*9*) concluded that "it is possible to determine progeny rows homozygous for earliness in F_3 and subsequent generations of hybrids by the time required for them to pass through the heading stage."

TABLE 25.—*Dates of heading of 2,017 F_3 plants of Marquis–Hard Federation wheat crosses, in comparison with the parents, grown at Bozeman and Havre, Mont., in 1924*

Date of heading	Bozeman			Havre		
	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Hard Federation	Marquis
July 4	24	21				
July 5	87	29				
July 6	155	29	1			
July 7	175	8	2		1	
July 8	73	1	1		17	
July 9	163	13	4	5	28	
July 10	61	2	6	52	36	
July 11	162	9	6	100	19	
July 12	96	4	1	124	10	
July 13	113	2	10	118	3	12
July 14	98	4	20	88	1	33
July 15	47	2	13	84		33
July 16	31		14	20		14
July 17	17	1	9	18		9
July 18	3		2	12		7
July 19	6		2	15		2
July 20	16		5	7		1
July 21	6		5	6		2
July 22	11		2	6		
July 23				2		1
July 24	4					
July 25	3		3			
July 26	6		2			
July 27	1					
July 28	1		2			
July 29						
July 30	1					
Total	1,360	125	110	657	115	114
Average date, July	10.2	7.0	15.4	13.3	9.9	15.3

In the present study the variability of the parent rows was in some cases greater than that of some of the hybrid strains. No sufficiently clear-cut differences in variability were obtained which could be used as a basis for separating the hybrids into homozygous early, homozygous late, or heterozygous groups. All of the hybrid plants labeled for date of heading are therefore combined, and the data, in comparison with the parents, are given in Table 25.

The data show that the hybrids exceed the parents in variability and with a much wider range of variation in the Bozeman data than in those from Havre. It is very apparent that time is not the only factor concerned in bringing wheat from first to fully headed. Temperature, sunlight, moisture, and soil-fertility factors may be of equal importance. The number of days required for all rows at Bozeman, Moccasin, and Havre to pass from first to fully headed are shown in Table 26.

TABLE 26.—*Heading period in the F_3 generation of 672 Marquis–Hard Federation wheat hybrids, in comparison with 79 parent checks, grown at Bozeman, Moccasin, and Havre, Mont., in 1924*

Heading period (time from first to fully headed)	Number of rows								
	Bozeman			Moccasin			Havre		
	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Hard Federation	Marquis
3 days							3		1
4 days				7		1	34		13
5 days	3			42	1	6	81		2
6 days	6		1	59	4	2	107	12	
7 days	8	1		30	3		51	6	1
8 days	15	2	1	12	1		17		
9 days	23	1	4				5		
10 days	21	1	2						
11 days	35	2	4						
12 days	27	3	1						
13 days	37	1							
14 days	28	1							
15 days	16	1							
16 days	2								
17 days	1								
18 days									
19 days	2								
Total	224	13	13	150	9	9	298	18	17
Average period in days	11.4	10.9	9.7	6.0	6.4	5.1	5.8	6.3	4.2

The data show that there are numerous hybrid strains which head within a shorter period than the average of the parents. The later heading Marquis parent has a shorter average heading period than the early-heading Hard Federation parent at all three stations. The length of the heading period, for both parents and hybrids, decreases with increasingly unfavorable environmental conditions from Bozeman to Havre.

Early heading was one of the objects for which these crosses were made. It is apparent that strains homozygous for relative date of heading were obtained by the F_3 generation and that some are nearly as early as the Hard Federation parent.

RIPENING PERIOD

In inheritance studies of maturity in several crosses Thompson (*19*) found that the date of ripening in the F_1 generation was near that of the mean of the later parent. In the F_2 generation most of the plants were intermediate between the parents, indicating blending. The apparent dominance of late ripening in the F_1 generation was explained as due to heterosis, and the further results on "the multiple determiner hypothesis of blending."

The plan of the present study was to determine the inheritance of earliness as measured both by date of heading and date of ripening, and also the importance of the intervening fruiting period. No comparison of the dates of ripening of the F_1 hybrids with those of the parents are available, but F_2 data are available from different

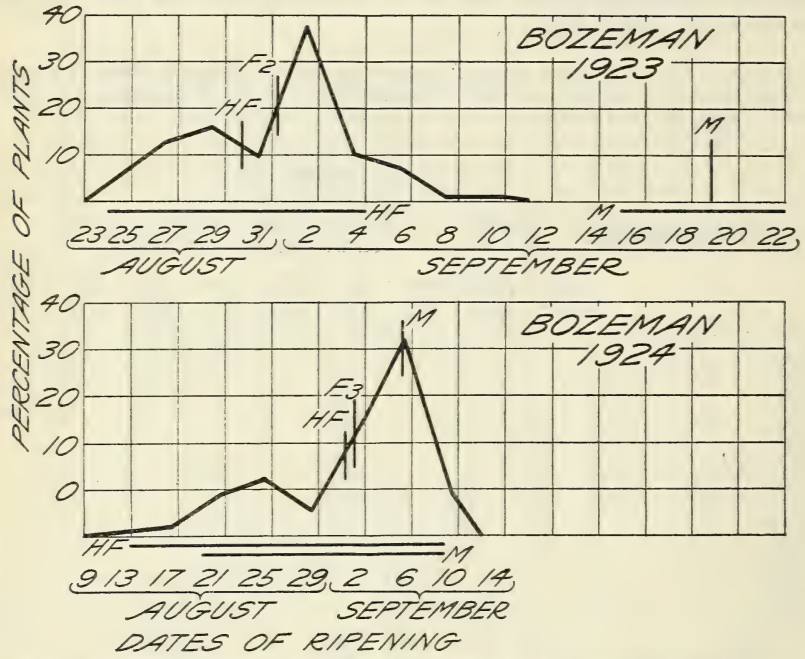

FIG. 3.—Frequency distribution of F_2 and F_3 hybrid wheat plants and the range of variation of the Marquis and Hard Federation parents, together with their average dates of ripening at Bozeman, Mont., in 1923 and 1924

families of reciprocal crosses grown at Bozeman and Moccasin in 1923. Unfortunately, the parent varieties were not grown at Moccasin.

The date of ripening was recorded when the last green color disappeared in the peduncle and the kernels were firm to the pinch of the thumb-nail. Kernels in the different heads of some plants varied from dead ripe to soft dough. For this reason maturity was determined by the average ripeness of the stems and kernels combined. The plants were harvested daily, and the date of ripening was recorded on the envelope in which heads from individual plants were placed. The data obtained in the F_2 generation are presented in Table 27 and the Bozeman data shown graphically in Figure 3.

The Bozeman data in Table 27 and Figure 3 indicate dominance of early ripening as the hybrids average less than 2 days later than

Hard Federation and nearly 19 days earlier than Marquis. However, because of a slight confusion in the planting plans, the Marquis parent was sown 2 days later and emerged 1 day later than the hybrids and Hard Federation. This, together with late rains and the fact that there was greater trampling of the soil between rows of the hybrids, caused Marquis to mature later, and the results are more extreme than would otherwise be the case.

TABLE 27.—*Segregation in the F_2 generation into 2-day frequency classes for the date of ripening of 1,039 plants of Marquis×Hard Federation and reciprocal wheat crosses grown at Bozeman and Moccasin, Mont., in 1923*

Station and time of ripening	Number of plants				
	F_2 hybrids			Hard Federation	Marquis
	Hard Federation×Marquis	Marquis×Hard Federation	Total		
Bozeman:					
August 24.5	19	11	30	13	
August 26.5	38	35	73	16	
August 28.5	38	55	93	19	
August 30.5	26	30	56	8	
September 1.5	118	104	222	39	
September 3.5	29	30	59	4	
September 5.5	19	22	41		
September 7.5	2	6	8		
September 9.5		1	1		
September 11.5					
September 13.5					
September 15.5					11
September 17.5					26
September 19.5					45
September 21.5					18
Total	289	294	583	99	100
Mean time and probable error:					
August	30.98±0.14	31.19±0.13	31.09±0.09	29.63±0.21	
September					18.9±0.12
Moccasin:					
August 10.5	1	4	5		
August 12.5					
August 14.5	8	2	10		
August 16.5	22	3	25		
August 18.5	14	12	26		
August 20.5	18	25	43		
August 22.5	25	26	51		
August 24.5	41	44	85		
August 26.5	35	40	75		
August 28.5	3	18	21		
August 30.5	36	36	72		
September 1.5	21	18	39		
September 3.5	2	2	4		
Total	226	230	456		
Mean time and probable error:					
August	24.54±0.24	25.40±0.21	24.98±0.16		

The reciprocal crosses show but slight, if any, maternal influence when compared with the data for date of heading. The Bozeman data show a difference between the reciprocal crosses of only 0.21 ± 0.19 days, which is 1.1 times its probable error, and indicates odds of but 1.2:1 that such a difference is due to chance alone. The Moccasin data have a difference of 0.86 ± 0.32 days, which is 2.7 times its error, indicating odds of only 13.6:1. Neither result, therefore, is statistically significant.

The variability for date of ripening was much greater than for date of heading, making it desirable to use 2-day frequency classes

in presenting the results. The F_2 hybrids again show greater variability than either of the parents, but the extreme dates of earliness or lateness of the parents were not exceeded by F_2 plants of the hybrids. Variability constants computed for the growing period, or days from emergence to ripening, are given in Table 28.

TABLE 28.—*Mean, standard deviation, and coefficient of variation for the growing period or days from emergence to ripening of F_2 wheat hybrids and for the Hard Federation and Marquis parents grown at Bozeman, Mont., in 1923*

Material compared	Mean	Standard deviation	Coefficient of variation
F_2 hybrid	91.09±0.09	3.298±0.065	3.621±0.072
Hard Federation	89.63± .21	3.136± .150	3.499± .168
Marquis	108.90± .12	1.725± .082	1.584± .076

The data show a slight but not a significantly greater variability for the hybrids than for the early and most variable Hard Federation parent, although the hybrids are significantly later. Because of the lateness of Marquis, variability for this variety was probably much less than normal.

TABLE 29.—*Dates when fully ripe in the F_3 generation of 672 Marquis–Hard Federation wheat hybrids, in comparison with 79 parent checks, grown at Bozeman, Moccasin, and Havre, Mont., in 1924*

Dates when fully ripe	Number of rows								
	Bozeman			Moccasin			Havre		
	F_3 hybrid	Hard Federation	Marquis	F_3 hybrid	Hard Federation	Marquis	F_3 hybrid	Hard Federation	Marquis
August 12							2		
August 13							9		
August 14							11		
August 15							26	6	
August 16				14	2		66	7	
August 17				15	3		89	1	1
August 18				17	3		38	2	8
August 19				29	1	1	21		3
August 20				26			17	1	3
August 21				17			17	1	2
August 22				21		1	2		
August 23				10		4			
August 24				1		3			
August 25									
August 26									
August 27	2	1							
August 28	16	4	1						
August 29	16	4							
August 30	14								
August 31	30	1							
September 1	34	2							
September 2	68		3						
September 3	33	1	7						
September 4	9		2						
September 5	2								
Total	224	13	13	150	9	9	298	18	17
Average time of ripening:									
August		29.5		19.5	17.3	22.8	17.0	16.4	18.8
September	1.0		2.5						

Three notes were taken for dates of ripening on F_3 rows at each station: (1) First ripe, (2) 50 per cent ripe, and (3) fully ripe. From a careful study of these notes it appears that fully ripe is the most definite and therefore the most valuable. The frequency data for date when fully ripe are shown for the three stations in Table 29 and graphically in Figure 4.

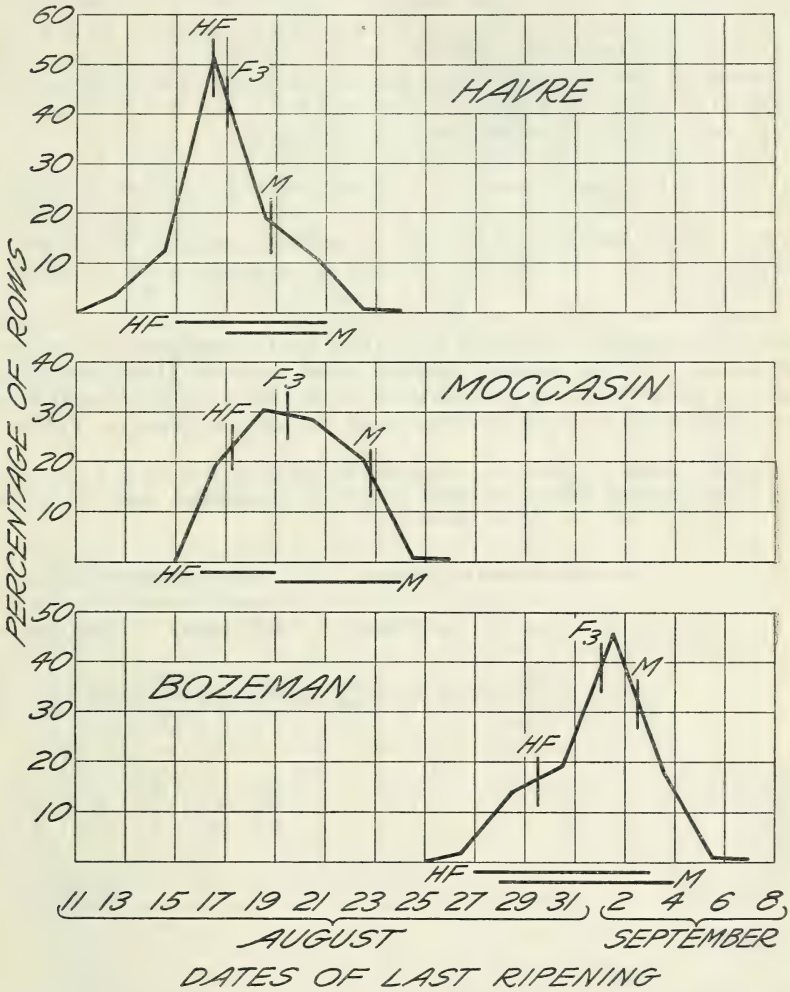

FIG. 4.—Frequency distribution of F_3 hybrid wheat strains and the range of variation of the Marquis and Hard Federation parents, together with their average dates of last ripening at Havre, Moccasin, and Bozeman, Mont., in 1924

The data show that most of the F_3 hybrids are intermediate between the parents, with the early and late extremes of the parents exceeded only by a few hybrid strains. The date of fully ripe on the F_3 row basis shows a greater variability for the hybrids in comparison with the parents than did the date of ripening on individual F_2 plants. Different rows of the parents, however, vary considerably at all stations for date of fully ripe. Figures 2 and 4 show that the

heading period at the three stations was in the order of Bozeman, Moccasin, and Havre, but that the ripening period was reversed, or in the order of Havre, Moccasin, and Bozeman. Drought, which resulted in forced ripening at Havre, caused this reversed ranking for the ripening period.

The dates of first ripening and 50 per cent ripe were of little value at Bozeman because of the damage from root-rot, which resulted in about 18 per cent of the hybrids ripening prematurely. At the other stations the dates of first and 50 per cent ripe gave no index in themselves as to strains which were homozygous. In the early and late classes the variability between first and fully ripe was frequently as great as in the intermediate frequency classes.

The same individual F_3 plants and families were noted for date of ripening as for date of heading. F_3 plant data for date of ripening in comparison with the parents, therefore, are available from two stations. There was not so marked a variation among the frequency distributions of the various families as was the case for date of heading.

Some of the earliest and latest ripening F_2 plants were included among the families studied in F_3. Data for the earliest of these rows, compared with the nearest labeled check rows of Hard Federation and the latest rows in comparison with the nearest labeled check row of Marquis at both Bozeman and Havre, are given in Table 30.

TABLE 30.—*Dates of ripening of individual F_3 plants from early and late strains of Marquis–Hard Federation wheat crosses, in comparison with the parents, grown at Bozeman and Havre, Mont., in 1924*

Time of ripening	Bozeman strain and row numbers						Havre strain and row numbers					
	Early ripening			Late ripening			Early ripening			Late ripening		
	B2–94; 226	B1–47; 230	Hard Federation; 220	B1–78; 2	B3–5; 23	Marquis; 10	B2–94; 159	B1–47; 316	Hard Federation; 300	B1–78; 26	A2–77; 72	Marquis; 10
August 11.5									8			
August 13.5		1	1				16	12	16	2		
August 15.5							19	13	27	29	12	41
August 17.5	2	3	5				2	13	1	16	21	23
August 19.5	6	1	6		1			1			2	1
August 21.5			1	1								
August 23.5	3			1	3							
August 25.5	1	2	6			1						
August 27.5	2	1	4			1						
August 29.5	1	9	1									
September 0.5		11	3									
September 2.5	3	1	6	1	4	1						
September 4.5		1	3	4	10	13						
September 6.5	10	4	11	22	24	28						
September 8.5			5	10	8	9						
Total	28	34	52	39	50	53	37	39	52	47	35	65
Average time of ripening:												
August	28.9	29.3	29.7				14.7	15.7	14.3	16.1	16.9	16.3
September				5.9	4.9	5.9						

Strain B2–94 was the earliest of 25 studied at Bozeman for date of ripening in 1924. This family was the progeny of one of the latest ripening F_2 plants, which ripened on September 6, 1923. The average date of ripening of Hard Federation in 1923 was August 30. In

F_3 strain B2–94 averaged earlier, although not significantly so, than the nearest labeled check row of Hard Federation. At Havre, however, the same strain averaged later than Hard Federation. Strain B1–47 was the second earliest strain studied at Bozeman in 1924 and also one of the earliest at Havre, this family being the progeny of an F_2 plant which ripened on September 1, 1923.

Among the late strains in F_3, A2–77 appeared significantly later than Marquis at Havre, the difference, 0.66 ± 0.16, being 4.1 times its error. At Bozeman, on the other hand, this strain averaged about two days earlier than Marquis. The F_2 parent of this strain ripened on September 2, 1923. The F_2 parents of the two latest F_3 strains at Bozeman, B1–78 and B3–5, also were not late-ripening plants in the F_2 generation, having ripened on August 24 and 27, respectively. Of the late strains at Bozeman B1–78 averaged equally as late as Marquis, but no strain was later than the late parent in average date of ripening.

The data as a whole can not be considered sufficient evidence to prove transgressive segregation, but are evidence of the importance of environment in determining all plant physiological responses.

TABLE 31.—*Dates of ripening of 1,681 F_3 plants of Marquis–Hard Federation wheat crosses, in comparison with the parents, grown at Bozeman and Havre, Mont., in 1924*

Station and time of ripening	F_3 hybrid	Hard Federation	Marquis
Bozeman:			
August 13.5	7	2	
August 15.5	7		
August 17.5	11	5	
August 19.5	73	9	2
August 21.5	9	1	
August 23.5	54	1	
August 25.5	56	11	3
August 27.5	27	5	1
August 29.5	25	1	
September 0.5	68	4	2
September 2.5	134	18	3
September 4.5	184	24	22
September 6.5	212	20	56
September 8.5	89	6	13
Total	956	107	102
Average time of ripening, September	1.2	.3	5.3
Havre:			
August 9		2	
August 10		2	
August 11	8	11	
August 12	29	16	
August 13	62	21	
August 14	106	18	
August 15	174	35	19
August 16	149	11	33
August 17	115	1	37
August 18	46		19
August 19	23		13
August 20	11		4
August 21	2		
Total	725	117	125
Average time of ripening, August	15.5	13.6	16.9

The variation in the number of days required for the different families to pass from first to fully ripe, when compared with the parents, is more striking than in the case of date of heading, partly

on account of greater variation of the parents. The data for all of the F_3 plants studied for date of ripening at Bozeman and Havre are compared in Table 31 with similar data from parent plants grown in duplicate check rows. The Bozeman data are illustrated in Figure 3.

At Bozeman the mean date of ripening of the hybrids is nearer that of Hard Federation; at Havre the mean of the hybrids is nearer that of Marquis, this latter fact being due probably to forced ripening of Marquis by drought. All F_3 data for date of ripening tend more toward an intermediate position in respect to the parents than toward a dominance of earliness, as was found for date of heading. Both F_2 and F_3 plant data for date of ripening in Figure 3 show bimodal curves, but no genetic importance can be given to this, as the parent varieties show the same types of curves, and the hybrids in F_2 at Moccasin and F_3 at Havre do not produce similar curves. Both date of heading and date of ripening data produce more or less skew curves with the mode for date of heading toward the early side and the mode for date of ripening toward the late side. As the same relationship holds true for the parents as well as the hybrids, it must be considered as due to environmental rather than genetic factors.

Homozygosity for date of ripening, like that for date of heading, is best expressed in terms of variability. The number of days required for all rows at Bozeman, Moccasin, and Havre to pass from first to fully ripe is shown in Table 32.

TABLE 32.—*Ripening period in the F_3 generation of 672 Marquis–Hard Federation wheat hybrids, in comparison with 79 parent checks, grown at Bozeman, Moccasin, and Havre, Mont., in 1924*

Ripening period (time from first to fully ripe)	Number of rows								
	Bozeman			Moccasin			Havre		
	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Hard Federation	Marquis
1 day							1		
2 days							26		3
3 days							64	1	4
4 days							89	6	5
5 days							75	6	4
6 days							33	3	1
7 days							5	2	
8 days							4		
9 days				18		1	1		
10 days				41	3				
11 days				27	2	2			
12 days				41	4	2			
13 days				18		4			
14 days	4	1		2					
15 days	23	1	1	1					
16 days	38	6	4	2					
17 days	38	1	3						
18 days	51	1	3						
19 days	32	2							
20 days	24		2						
21 days	12	1							
22 days	1								
23 days	1								
Total	224	13	13	150	9	9	298	18	17
Average period in days	17.7	16.8	17.2	11.1	11.1	11.9	4.2	4.9	3.8

The data show very contrasting differences in the ripening period at the three stations and that there are numerous hybrid strains

which ripen in a shorter number of days than the average period of the parents. The earlier ripening Hard Federation parent ripened in a shorter period than the later ripening Marquis parent at two of the three stations. Among the check rows of parents the variation in days from first to fully ripe is less at two of the three stations than the average ripening period. In general, about half of the F_3 hybrid families ripened in a period equal to or less than the average of the parents. It is not possible to separate the hybrid material with sufficient accuracy, however, to make a genetic interpretation.

Late ripening was one of the objects for which these studies were made, and from a breeding standpoint it is apparent that homozygous strains for the ripening period have been obtained by the F_3 generation and that some strains are as late or later ripening than the late Marquis parent.

FRUITING PERIOD

The term "fruiting period" as a designation for the number of days from heading to ripening was first used by Carleton (*4, p. 275*) in 1905. He later emphasized its importance "as the most critical period in the life of the crop" and called attention to "the correlations existing between the length of this period and certain other characteristics of the crop, as yield and protein content."

As early as 1893 Schindler (*16*) had observed that—

> With the length of the vegetative period, especially in respect to the length of the interval between flowering and ripening, not only does the dimension of the kernel increase but the amount of carbohydrates stored therein increases and the protein content decreases.

Thatcher (*18, pp. 39–47*) and his students studied this problem with plants from four varieties and found that the average weight of kernel varies directly and the percentage of nitrogen inversely with the length of the fruiting period.

Since 1915, among other data, the length of the fruiting period has been recorded (C. I. form No. 13) in all varietal experiments conducted by the Office of Cereal Investigations. During the first three years, 1920 to 1922, inclusive, that Hard Federation was included in the varietal experiments at Moccasin, it outyielded Marquis by an average of 6.2 bushels per acre. R. W. May, assistant agronomist, in charge of the experiments, noted that each year the higher yield of Hard Federation was associated with a longer fruiting period. During these three years the average fruiting period of Marquis was 29 days and that of Hard Federation 37 days, a difference of 8 days. The results with these two varieties appeared to be an outstanding instance of the probable positive correlation of the relative length of fruiting period with yield. The present study, accordingly, was outlined partly to determine the inheritance of modification in length of the fruiting period, but more particularly to determine its interrelationships with the heading period and the ripening period and its importance from a breeding standpoint in affecting the yield and crude-protein content of hybrid strains.

No comparison of the fruiting periods of the F_1 hybrids with those of the parents was attempted. The F_2 data obtained are not comparable with those of the Marquis parent, because of the confusion in the seeding plans previously mentioned. The fruiting

period of individual F_2 plants from reciprocal crosses was studied, however, and these data in comparison with those of the Hard Federation parent are presented in Table 33 and graphically in Figure 5.

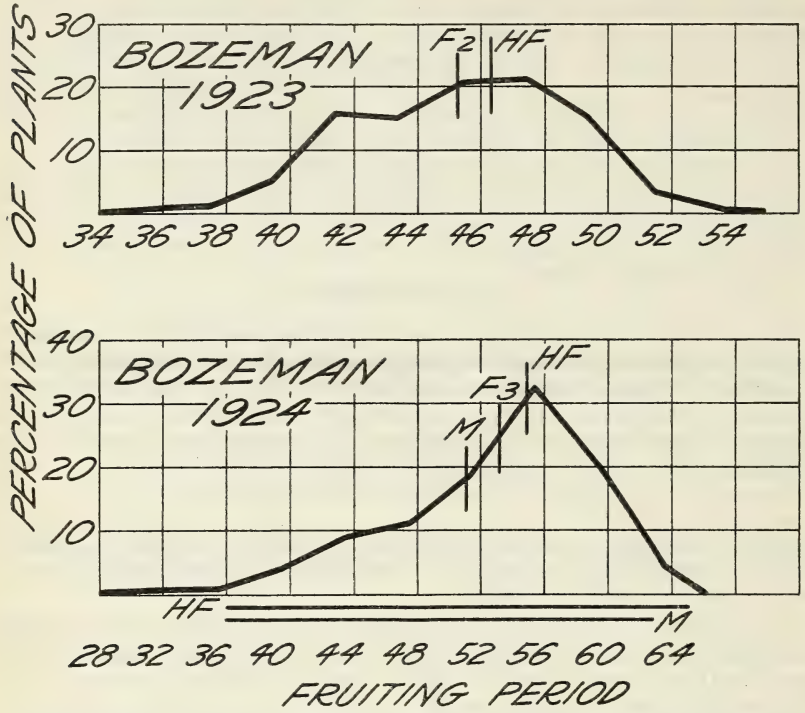

FIG. 5.—Frequency distribution of F_2 and F_3 hybrid wheat plants and the range of variation of the Marquis and Hard Federation parents, together with their average fruiting periods at Bozeman, Mont., in 1923 and 1924

TABLE 33.—*Segregation in the F_2 generation into 2-day frequency classes for fruiting period of 583 plants of Marquis–Hard Federation wheats and reciprocal crosses, in comparison with the Hard Federation parent, grown at Bozeman, Mont., in 1923*

Fruiting period (time from heading to ripening)	Number of plants			
	F_2 hybrids			Hard Federation
	Hard Federation × Marquis	Marquis × Hard Federation	Total	
35.5 days		1	1	
37.5 days	2	7	9	
39.5 days	18	14	32	4
41.5 days	41	51	92	11
43.5 days	43	45	88	10
45.5 days	50	74	124	26
47.5 days	71	57	128	21
49.5 days	52	34	86	18
51.5 days	12	10	22	8
53.5 days		1	1	1
Total	289	294	583	99
Mean period in days and probable error	45.67±.13	45.07±.13	45.37±.09	46.33±.22

The data show that in the F_2 generation the fruiting period of the hybrids averaged 0.96 ± 0.24 days shorter than that of Hard Federation. This difference, which is 4.0 times its probable error, is signifi-

cant. Reciprocal crosses show what might be interpreted as slight maternal influence, the Hard Federation × Marquis crosses averaging 0.60 ± 0.18 days longer in fruiting period than crosses of Marquis × Hard Federation. This difference is 3.3 times its probable error.

The variability of the hybrids appears slightly greater than that of Hard Federation, and their coefficients of variability are as follows:

	Coefficient of variation
F_2 hybrids	7. 295 ± 0. 144
Hard Federation	6. 915 ± . 331
Difference	. 380 ± . 361

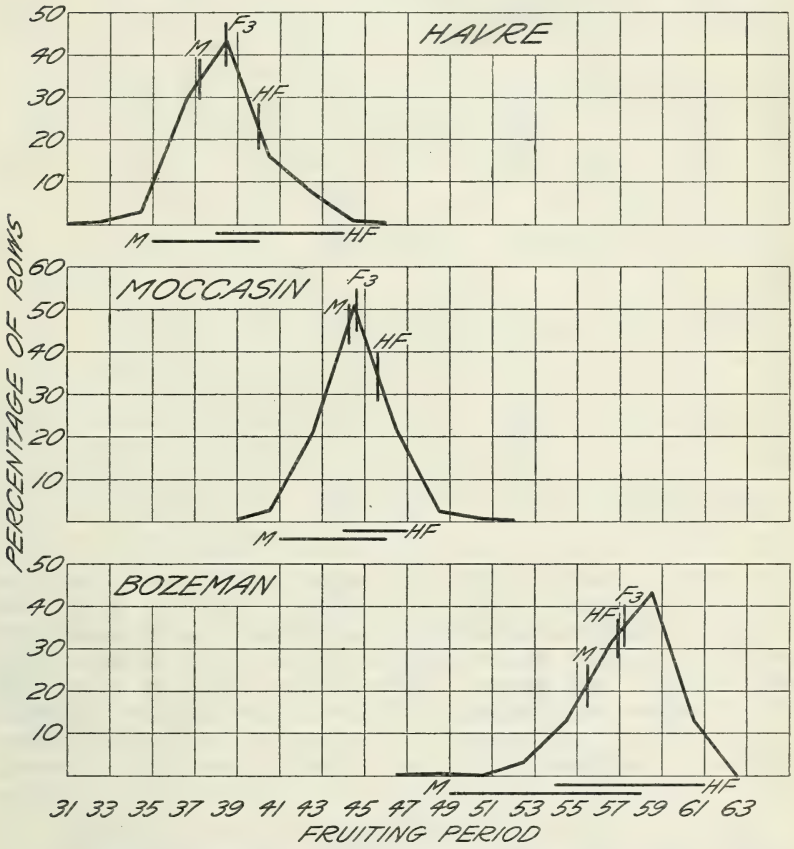

FIG. 6.—Frequency distribution of F_3 hybrid wheat strains and the range of variation of the Marquis and Hard Federation parent checks, together with their average fruiting periods at Havre, Moccasin, and Bozeman, Mont., in 1924

As the difference is only about once the error, the variability of the hybrids can not be said to be significantly different from that of Hard Federation.

The fruiting periods of F_3 strains and parent checks grown in rod rows in 1924 at Bozeman, Moccasin, and Havre were computed from the date of first heading to the date when fully ripe. The frequency data obtained are shown for the three stations in Table 34 and graphically in Figure 6.

TABLE 34.—*Fruiting period in the F_3 generation of 672 Marquis–Hard Federation wheat hybrids, in comparison with 79 parent checks, grown at Bozeman, Moccasin, and Havre, Mont., in 1924*

Fruiting period	Number of rows								
	Bozeman			Moccasin			Havre		
	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Hard Federation	Marquis
32 days							1		
33 days									
34 days									
35 days							10		1
36 days							25		7
37 days							61		2
38 days							71	3	3
39 days							60	7	3
40 days				1			30	3	1
41 days				3		1	17	2	
42 days				9			17	1	
43 days				22			5	1	
44 days				30	1	3	1	1	
45 days				47	4	4			
46 days				23	2	1			
47 days				10	2				
48 days				3					
49 days	1		1	1					
50 days				1					
51 days									
52 days	4								
53 days	4								
54 days	9		1						
55 days	21	4	3						
56 days	29	3	4						
57 days	40	3	3						
58 days	63		1						
59 days	35	1							
60 days	15	1							
61 days	3	1							
Total	224	13	13	150	9	9	298	18	17
Average period in days	57.2	56.8	55.5	44.6	45.6	44.3	38.4	39.9	37.2

The data in Table 34 show the longer fruiting period of Hard Federation as compared with that of Marquis. At two of the three stations the mean fruiting period of the hybrids was intermediate to those of the parents, but at Bozeman the mean of the hybrids exceeded those of both parents. The fruiting period on a row basis in the F_3 generation illustrated in Figure 6 shows greater variability for the hybrids in comparison with the parents than did the fruiting period on an individual plant basis in the F_2 generation. The wide variation in fruiting period at the three stations is most striking, showing environmental effect due to differences in moisture, temperature, soil fertility, etc. The length of the fruiting period was increased with the more favorable environmental conditions from Havre to Moccasin and to Bozeman.

Selections were made from the F_2 generation based on the length of fruiting period. The progeny of some of the F_2 plants of longest fruiting period were included among the families studied on an individual-plant basis in the F_3 generation. From these, data on rows having the longest and shortest fruiting period, in comparison with the nearest studied parent check rows at Bozeman and Havre, are given in Table 35.

The fruiting period in the F_3 generation of strain A2–77 was the shortest of any studied at Bozeman and averaged 3.58 ± 0.86 days

less than that of the nearest studied Marquis check. This difference is about 4.2 times its error. At Havre, however, this same strain averaged only 0.2 day shorter in fruiting period than Marquis, indicating the importance of environment in regulating such physiologic behavior. Strain B1–78 was significantly shorter in fruiting period than Marquis at both stations, the difference at Bozeman being 2.56 ± 0.61 days and at Havre 4.36 ± 0.59 days. The strain of next shortest fruiting period at Havre was B2–93, but the fruiting period of this strain was not significantly shorter than that of Marquis. In the F_2 generation the mother plant of strain B2–93 had a long fruiting period, 51 days, in contrast to strains B1–78 and A2–77, whose mother plants in the F_2 generation had short fruiting periods of 38 and 41 days, respectively.

TABLE 35.—*Fruiting period of individual F_3 plants of short and long fruiting strains of Marquis–Hard Federation wheat crosses, in comparison with the parents, grown at Bozeman and Havre, Mont., in 1924*

Fruiting period	Bozeman strain and row Nos.						Havre strain and row Nos.					
	Short fruiting			Long fruiting			Short fruiting			Long fruiting		
	A2–77; 17	B1–78; 4	Marquis; 10	A1–34; 45	B1–65; 113	Hard Federation; 20	B2–93; 158	B1–78; 26	Marquis; 10	A3–101; 308	B1–65; 203	Hard Federation; 300
22.5 days								1				
24.5 days							4	4				
26.5 days							3	3	3			
28.5 days							4	2	3			
30.5 days	1						12	4	8			5
32.5 days							3	1	34	2	3	4
34.5 days	2						7	1	14	12	17	13
36.5 days						1	2			17	12	27
38.5 days		1				1				7	6	2
40.5 days	2					2					1	
42.5 days	1	5	1		4							
44.5 days	2	2	1	2	1							
46.5 days	2	2	3	3	1	2						
48.5 days	3	4	4	7		1						
50.5 days	2	3	7		2	1						
52.5 days	9	11	15		6	7						
54.5 days	7	8	12	3	6	9						
56.5 days	1	2	6	2	11	7						
58.6 days	1		2	5	9	7						
60.5 days			1	4	4	7						
62.5 days			1	8	4	7						
64.5 days				2	1	2						
Total	33	38	53	36	49	54	35	16	62	38	39	51
Average period in days	49.1	50.1	52.7	55.8	55.3	55.6	30.6	27.9	32.2	36.0	35.7	35.2

The three F_3 strains of longest fruiting period at both stations, A1–34, B1–65, and A3–101, were the progeny of F_2 plants with fruiting periods of 43, 47, and 52 days, respectively, in 1923. The average fruiting period of Hard Federation in 1923 was 46 days. Of seven plants having the longest fruiting period in the F_2 generation, none averaged the longest in F_3 of 25 strains studied at Bozeman in 1924. Strain A1–34 was longest in fruiting period at Bozeman, but at Havre it had a slightly shorter fruiting period than Marquis. Strain B1–65 slightly exceeded Hard Federation in average length of fruiting

period at Havre, but not at Bozeman. At neither station were the differences significant. Strain A3–101 also slightly exceeded Hard Federation at Havre, but no strain studied was significantly longer than Hard Federation in fruiting period.

All of the F_3 plants studied for fruiting period among 25 rows at Bozeman and 16 rows at Havre are compared with those from duplicate rows of both parents in Table 36. The Bozeman data are shown in Figure 5.

TABLE 36.—*Fruiting period of 1,698 F_3 plants of Marquis–Hard Federation wheat crosses, in comparison with the parents, grown at Bozeman and Havre, Mont., in 1924*

Station and fruiting period	F_3 hybrid	Hard Federation	Marquis
Bozeman:			
30.5 days	1		
32.5 days	1		
34.5 days	4		
36.5 days	1	1	1
38.5 days	7	1	
40.5 days	32	4	5
42.5 days	47	3	4
44.5 days	46	3	3
46.5 days	40	6	6
48.5 days	74	2	7
50.5 days	67	4	16
52.5 days	128	15	21
54.5 days	154	10	22
56.5 days	185	12	8
58.5 days	134	14	2
60.5 days	76	13	1
62.5 days	40	13	1
64.5 days	4	5	
Total	1,041	106	97
Average period in days	53.3	55.0	51.2
Havre:			
22 days	1		
23 days	1		
24 days	3		
25 days	11		
26 days	5		2
27 days	9		2
28 days	9		1
29 days	15		3
30 days	42	2	8
31 days	52	6	7
32 days	92	6	23
33 days	97	12	33
34 days	113	25	20
35 days	92	19	13
36 days	58	21	1
37 days	31	19	
38 days	20	3	1
39 days	5	2	
40 days	1		
Total	657	115	114
Average period in days	33.1	34.8	32.6

These results confirm the data from F_2 plants and F_3 rows and show that the hybrids are intermediate to the parents in fruiting period. Several hybrid plants at both stations have a shorter fruiting period than any of the Marquis plants; only one plant, and that at Havre, had a longer fruiting period than the most extreme Hard Federation plants. Little or no evidence is presented, therefore, to show transgressive segregation for hybrids of longer fruiting period

than that of Hard Federation. It was possible, on the other hand, to obtain strains having a shorter fruiting period than that of Marquis.

HEIGHT

Stature, or height, is an agronomic problem in wheat production on the dry lands of Montana. Plate 1 illustrates the difference in height of Marquis (*A*) and Hard Federation (*B*) grown in the varietal plat experiments at Bozeman. Hard Federation frequently is not tall enough for convenient harvesting. A knowledge of the inheritance of height and its effect on production under different conditions is important.

Freeman (*10*), in a durum-common wheat cross, found the F_1 hybrids taller than the taller parent and a wide segregation for height in the F_2 generation. In Kota–Hard Federation crosses Clark (*5*) found that tallness appeared partially dominant but was due principally to heterosis and also easily affected by environmental conditions.

Data for reciprocal crosses in the F_2 generation are available from Bozeman and Moccasin, and those from Bozeman are comparable with the parent varieties. The F_2 plant data are given in Table 37 and are shown graphically in Figure 7. All dwarf plants were omitted from this study. Height was measured from the base of the culms to the tip of the spike, not including the awnlets of awnletted strains.

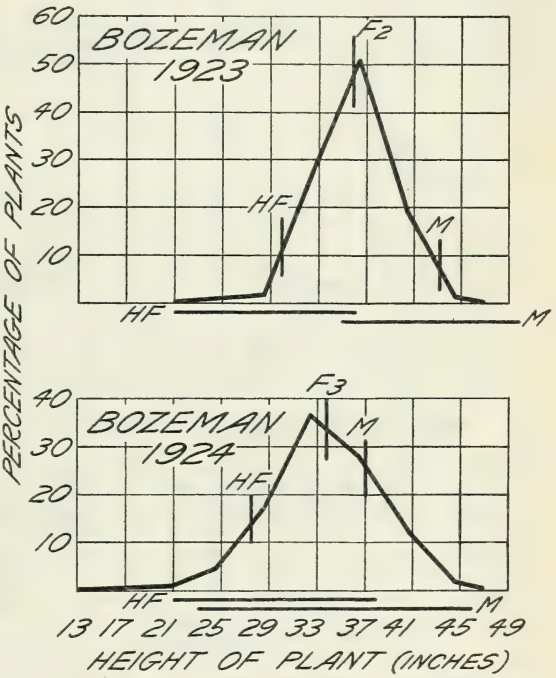

FIG. 7.—Frequency distribution of F_2 and F_3 hybrid wheat plants and the range of variation of the Marquis and Hard Federation parents, together with their average height at Bozeman, Mont., in 1923 and 1924

The data in Table 37 show that the F_2 hybrids are intermediate in height with the parents and with a greater range than either. None of the hybrids, however, attained the extremes in height and shortness reached by some parent plants.

The reciprocal crosses show what might be considered as a slight maternal influence at Moccasin and a paternal influence at Bozeman. In each case the differences between the reciprocal crosses are somewhat more than three times their probable errors, but in view of their opposite tendencies it is doubtful whether either is due to inherent causes.

TABLE 37.—*Segregation in the F_2 generation into 2-inch frequency classes for height of 1,043 plants of Marquis-Hard Federation and reciprocal wheat crosses grown at Bozeman and Moccasin, Mont., in 1923*

Height of plant	Bozeman					Moccasin		
	Hard Federation × Marquis	Marquis × Hard Federation	Total	Hard Federation	Marquis	Hard Federation × Marquis	Marquis × Hard Federation	Total
21.5 inches				1				
23.5 inches		1	1					
25.5 inches		1	1	5				
27.5 inches	1	1	2	21		4	1	5
29.5 inches	4	4	8	28		4		4
31.5 inches	22	31	53	30		12	9	21
33.5 inches	46	60	106	13		28	23	51
35.5 inches	68	86	154	1	3	47	46	93
37.5 inches	72	71	143		7	54	50	104
39.5 inches	55	30	85		8	51	60	111
41.5 inches	19	8	27		21	22	28	50
43.5 inches	5	1	6		26	3	11	14
45.5 inches	1		1		22		3	3
47.5 inches					12			
49.5 inches					1			
Total	293	294	587	99	100	225	231	456
Mean height in inches and probable error	36. 58±. 12	35. 57±. 11	36. 07±. 08	29. 98±. 16	43. 08±. 21	36. 87±. 14	37. 82±. 14	37. 35±. 10

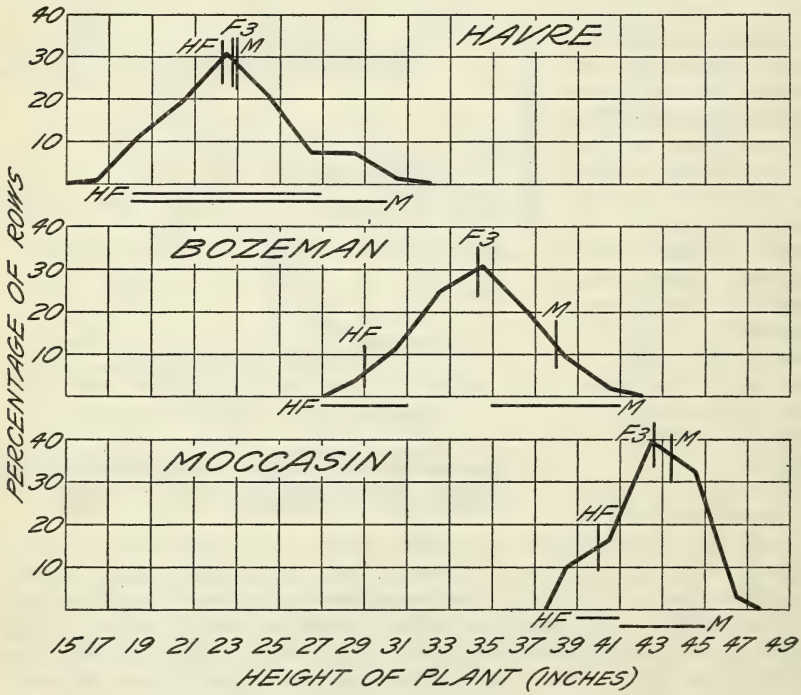

FIG. 8.—Frequency distribution of F_2 hybrid wheat strains and the range of variation of the Marquis and Hard Federation parent checks, together with their average height at Havre, Bozeman, and Moccasin, Mont., in 1924

The variability of the hybrids in comparison with the parents as determined by coefficients of variability is as follows:

	Coefficient of variation
F_2 hybrids	8. 194 ± 0. 161
Hard Federation	7. 994 ± . 383
Marquis	7. 171 ± . 342

These data show that Hard Federation is slightly more variable than Marquis, but this variability is due principally to the difference in their mean heights. The hybrids also are slightly more variable than Hard Federation, but they are not significantly more variable even than Marquis.

In 1924, height notes were recorded for nursery rows of F_3 strains and parent checks grown at Bozeman, Moccasin, and Havre. The frequency data obtained are given in Table 38 and are shown graphically in Figure 8.

TABLE 38.—*Height in the F_3 generation of 673 Marquis–Hard Federation wheat hybrids, in comparison with 79 parent checks grown in nursery rows at Bozeman, Moccasin, and Havre, Mont., in 1924*

Average height of row	Number of rows								
	Bozeman			Moccasin			Havre		
	F_3 hybrid	Hard Federation	Marquis	F_3 hybrid	Hard Federation	Marquis	F_3 hybrid	Hard Federation	Marquis
16 inches							1		
17 inches							2		
18 inches							11	1	1
19 inches							24		2
20 inches							21	2	1
21 inches							38	6	2
22 inches							41	3	1
23 inches							51	2	4
24 inches							41	1	1
25 inches							21		1
26 inches							17	1	2
27 inches		3					6		1
28 inches	2	2					16	2	
29 inches	5	4					5		
30 inches	9	1					4		1
31 inches	16	3							
32 inches	25								
33 inches	30								
34 inches	29								
35 inches	39		1						
36 inches	25		2						
37 inches	21		2						
38 inches	11		4	4					
39 inches	9		2	10	4				
40 inches	3			6	2				
41 inches			2	18	3	1			
42 inches				30					
43 inches				29		4			
44 inches				34		2			
45 inches				15		2			
46 inches				4					
Total	224	13	13	150	9	9	299	18	17
Average height in inches	34. 3	28. 9	37. 9	42. 5	39. 9	43. 4	22. 8	22. 3	22. 9

The data give further evidence of the intermediate nature of the height of hybrids between that of the parents.

The differences in height of both hybrids and parents at the three stations strikingly show the effect of environment on height. At

Havre, Marquis averaged less than an inch taller than Hard Federation, and there was an average difference of 9 inches at Bozeman and of 3.5 inches at Moccasin. Figure 8 shows that the height increased at the stations in the order—Havre, Bozeman, and Moccasin. Earlier seeding probably accounts for the greater height at Moccasin than at Bozeman. The height of row in the F_3 generation indicates a greater variability for the hybrids in comparison with the parents than the height of plants in F_2. At Moccasin and Havre the extreme short and at Moccasin the extreme tall rows of the parents were exceeded by rows of the hybrids.

Selections were made in the F_2 generation on a height basis, and some of the tallest F_2 plants were included among the strains studied on the individual plant basis in F_3. The tallest and shortest of these strains, compared with the nearest studied parent rows at Bozeman and Havre, are given in Table 39.

TABLE 39.—*Height of individual F_3 plants of short and tall strains of Marquis–Hard Federation wheat crosses, in comparison with the parents, grown at Bozeman and Havre, Mont., in 1924*

Height of plant	Bozeman strain and row Nos.						Havre strain and row Nos.					
	Short stature			Tall stature			Short stature			Tall stature		
	B3–7; 24	B3–29; 27	Hard Federation; 20	B1–78; 4	A2–77; 17	Marquis; 10	A1–24; 169	B1–78; 26	Hard Federation; 40	B1–47; 316	B1–65; 203	Marquis; 290
11.5 inches							2					
13.5 inches							7	1	2			
15.5 inches							6	14	1			1
17.5 inches							8	18	12		1	3
19.5 inches							8	12	25	2		8
21.5 inches	1						9	2	18	3	2	9
23.5 inches	3	2	8		1		8		5	7	6	16
25.5 inches	1	1	7				2		2	10	18	16
27.5 inches	9	5	16	1						10	7	3
29.5 inches	6	14	25		2	1				6	3	4
31.5 inches	7	10	4	1	1	2				1	2	
33.5 inches	5	10	1	5								
35.5 inches				5	10	3						
37.5 inches			1	10	9	21						
39.5 inches				16	12	18						
41.5 inches				10	9	12						
43.5 inches				5	7	4						
45.5 inches				1	1	1						
Total	32	42	62	54	52	62	50	47	65	39	39	60
Average height in inches	29.1	30.3	28.1	38.7	38.5	39.0	18.8	17.5	19.9	25.8	25.7	23.4

Strain B1–78 was the tallest of those studied at Bozeman and the shortest at Havre. In the F_2 generation the parent plant of this strain was 39 inches tall when the average height of Hard Federation was 30 inches and that of Marquis 43 inches. This is an important example of the wide variations that may be obtained for height under different environmental conditions. None of the progenies of the tallest F_2 plants ranked among the tallest at either Bozeman or Havre. The second tallest F_3 strain at Bozeman, A2–77, is the progeny of an F_2 plant 34 inches tall. Strain B1–47, the parent plant of which was 36 inches tall in the F_2 generation, was the tallest

of 16 strains at Havre. Strain B1–65, the second tallest strain at that station, is the progeny of an F_2 plant only 33 inches tall.

Of the short F_3 strains, only B1–78 at Havre was significantly shorter than the nearest labeled check row of Hard Federation. As this same strain was the tallest of 25 F_3 strains at Bozeman, it is apparent that drought caused the shortness of this strain at Havre. The other short F_3 strains were not significantly shorter than Hard Federation, and at Bozeman none were as short. On a plant basis, only at Havre under unfavorable conditions was there any indication of transgressive inheritance for height of F_3 strains, and as these plants were not of normal stature little importance is given to the results being due to inherent causes.

All F_3 hybrid plants studied for date of heading, ripening, and consequent length of fruiting period were measured also for height. These data in comparison with the heights of individual plants from duplicate parent check rows are given in Table 40.

TABLE 40.—*Height of 2,021 F_3 plants of Marquis–Hard Federation wheat crosses, in comparison with the parents, grown at Bozeman and Havre, Mont., in 1924*

Height of plant	Bozeman			Havre		
	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Hard Federation	Marquis
11.5 inches				2		
13.5 inches				10	2	
15.5 inches				40	1	4
17.5 inches	1			70	12	18
19.5 inches	2			127	26	44
21.5 inches	7	1		151	26	19
23.5 inches	25	14	1	153	21	16
25.5 inches	29	29	1	103	24	16
27.5 inches	67	35	3	45	4	3
29.5 inches	145	33	4	22	1	4
31.5 inches	241	12	9	3		
33.5 inches	230	1	9			
35.5 inches	157		9			
37.5 inches	203	1	39			
39.5 inches	115		22			
41.5 inches	52		14			
43.5 inches	19		4			
45.5 inches	2		1			
Total	1,295	126	116	726	117	124
Average height in inches	33.79	27.58	36.95	21.94	21.91	21.19

The F_3 plant data from Bozeman given in Table 40 are shown graphically in Figure 7. These data confirm the F_2 plant and F_3 row data in showing that the hybrids are intermediate to the parents. The variability of F_3 plants also is not greater than that of the Marquis parent.

At Havre, Hard Federation was slightly taller than the Marquis parent, on account of droughty conditions, and the F_3 hybrids slightly taller than both parents. The variability in height of the hybrids and parents at Havre was practically the same.

From the F_2 and F_3 studies it may be concluded that height is inherited in intermediate degrees and without significantly greater variability than that of the parents. The respective heights of the

parents have been approximately reached by F_3 strains, but not exceeded significantly except under unfavorable conditions. This blending inheritance apparently is due to multiple genetic factors.

YIELD

Yield is a character complex, the product of genetic and environmental factors. The morphological and quantitative characters previously discussed are measures of preliminary plant response and are important because of their relationship to yield and quality. Yield is the end result of agronomic research. Beaven (*1*) has stated that "the problem of the cereal breeder is to discover the relation between the different structures of the individual plant and the probable quantity of salable produce per acre." This has been one of the primary objects of the present study.

Grain yields on a plant basis in the F_2 and F_3 generations and on a nursery-row basis in the F_3 generation were recorded. Yields were obtained from definitely spaced plants, which were harvested, threshed, and weighed individually. The F_2 data from Bozeman and Moccasin are given in Table 41 and the Bozeman results are shown graphically in Figure 9. Unfortunately, as previously stated, the parents were not grown with this generation at Moccasin.

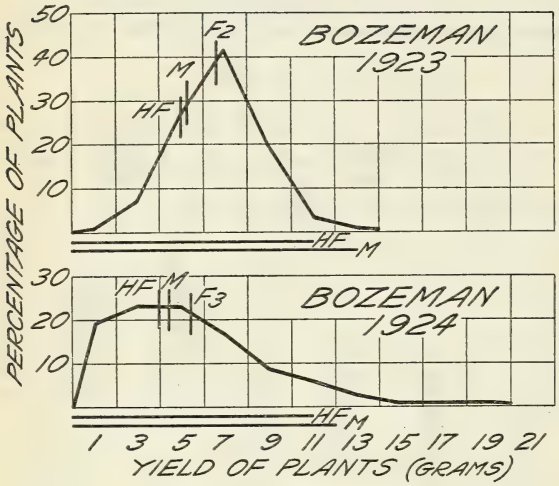

FIG. 9.—Frequency distribution of F_2 and F_3 hybrid wheat plants and the range of variation of the Marquis and Hard Federation parents, together with their average yield at Bozeman, Mont., in 1923 and 1924

The Bozeman data show that in the F_2 generation the hybrids averaged considerably above either parent in yield. Marquis slightly outyielded Hard Federation, but not by a significant amount. There is a consistent difference in the yield of reciprocal crosses at the two stations in that the Marquis × Hard Federation crosses outyielded those of Hard Federation × Marquis. For the Bozeman data the difference, 0.34 ± 0.11, is significant; but for the Moccasin data the difference, 0.45 ± 0.28, is only 1.6 times its error. The coefficients of variation which follow show that the F_2 hybrids are less variable in yield than either parent.

	Coefficient of variation
F_2 hybrids	28.267 ± 1.557
Hard Federation	34.470 ± 1.661
Marquis	43.845 ± 2.091

Nursery-row yields of F_3 strains and of parent checks were computed to an acre basis for Bozeman and Moccasin. Because of the dwarf plants occurring in some F_3 strains, a uniform number of

normal plants was not present in each row. At Bozeman and Havre a definite number of plants was grown in each row, and yields also have been computed per plant. This was not possible with the Moccasin data, seeding at this station not being definitely spaced. The data obtained by both methods, distributed in frequency classes, are given in Tables 42 and 43 and shown graphically in Figure 10.

TABLE 41.—*Segregation in the F_2 generation into frequency classes for yield of 1,045 plants of Marquis–Hard Federation and reciprocal wheat crosses grown at Bozeman and Moccasin, Mont., in 1923*

Yield per plant	Bozeman					Moccasin		
	F_2 hybrids			Hard Federation	Marquis	F_2 hybrids		
	Hard Federation × Marquis	Marquis × Hard Federation	Total			Hard Federation × Marquis	Marquis × Hard Federation	Total
0.5 gram	1		1	1		1	1	2
1.5 grams		4	4	2	5	5	7	12
2.5 grams	4	5	9	6	12	15	4	19
3.5 grams	14	19	33	16	15	25	9	34
4.5 grams	35	19	54	27	19	21	18	39
5.5 grams	59	46	105	20	14	17	12	29
6.5 grams	72	66	138	14	8	9	15	24
7.5 grams	52	56	108	6	15	15	30	45
8.5 grams	30	38	68	4	8	9	22	31
9.5 grams	22	24	46	1	1	29	35	64
10.5 grams	4	11	15	1		22	22	44
11.5 grams		4	4		2	18	15	33
12.5 grams		2	2		1	5	13	18
13.5 grams						13	3	16
14.5 grams						9	7	16
15.5 grams						6	7	13
16.5 grams						2	1	3
17.5 grams						2	3	5
18.5 grams							1	1
19.5 grams						1		1
20.5 grams							2	2
21.5 grams						1	2	3
22.5 grams						1	1	2
23.5 grams								
24.5 grams								
25.5 grams								
26.5 grams						1		1
27.5 grams								
28.5 grams								
29.5 grams								
30.5 grams						1		1
Total	293	294	587	98	100	228	230	458
Mean yield in grams and probable error	6.50±.07	6.84±.08	6.67±.05	5.06±.12	5.30±.16	8.47±.21	8.92±.18	8.70±.14

The Bozeman row data show that the yields of the F_3 hybrids average between the average yields of the parent check rows. The Moccasin data show that the average yield of the hybrids is less than that of both the parent checks. At both stations in 1924 Marquis outyielded Hard Federation. Largely because of the smaller number of check rows the hybrids appear to be much more variable in yield than the parent varieties. At both stations the extreme high and low yields of check rows were exceeded by hybrid strains.

At Moccasin, as previously noted, the plants were not definitely spaced, the rows being sown at the rate of 2.3 grams per rod row. Stands were not uniform, principally because of the dwarf plants

which appeared in different ratios in some of the hybrid strains. The yields of the rows producing these dwarfs were compared with the yields of rows in which no dwarfs appeared. The result follows:

	Average acre yield (bushels)
F_3 hybrids having no dwarfs	29.49 ± 0.38
F_3 hybrids having dwarfs	26.88 ± .47
Difference	2.61 ± .60

The difference, 2.61 ± 0.60 bushels, is significant. Dwarfs, therefore, were a factor in the low yields of the F_3 hybrids when compared with the parents on a row basis.

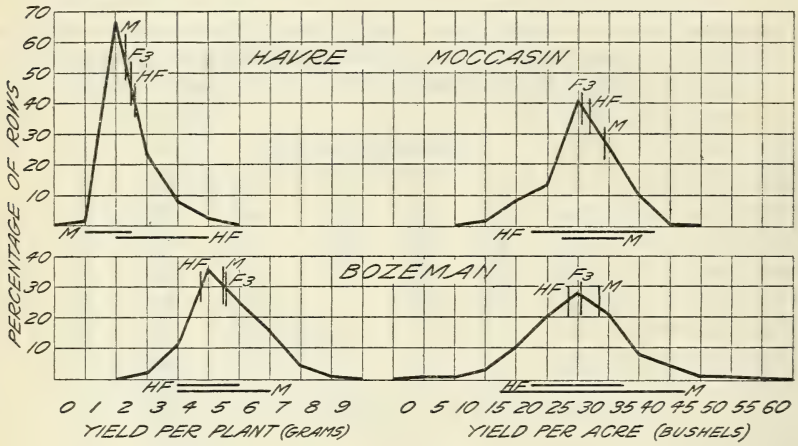

FIG. 10.—Frequency distribution of F_3 hybrid wheat strains and the range of variation of the Marquis and Hard Federation parent checks, together with their average yield per plant at Havre and Bozeman and yield per acre at Moccasin and Bozeman in 1924

TABLE 42.—*Yield per acre in the F_3 generation of 374 Marquis–Hard Federation wheat hybrids, in comparison with 44 parent checks grown in nursery rows at Bozeman and Moccasin, Mont., in 1924*

Yield per acre	Number of rows					
	Bozeman			Moccasin		
	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Hard Federation	Marquis
2.5 bushels	1					
7.5 bushels	1					
12.5 bushels	7			2		
17.5 bushels	24		2	12		
22.5 bushels	46	7	2	20	2	
27.5 bushels	63	3	1	61	4	3
32.5 bushels	48	3	4	39		6
37.5 bushels	19		3	15	3	
42.5 bushels	10		1	1		
47.5 bushels	2					
52.5 bushels	2					
57.5 bushels	1					
Total	224	13	13	150	9	9
Average yield in bushels	27.86	25.96	30.19	28.23	29.72	30.83

Differences in the competitive ability of normal and dwarf plants may introduce a variable into the data for average plant yield, but it seems doubtful whether this variable had any very pronounced effect on the result. Average plant-yield data are given in Table 43.

TABLE 43.—*Yield per plant in the F_3 generation of 523 Marquis–Hard Federation wheat hybrids, in comparison with 61 parent checks grown in nursery rows at Bozeman and Havre, Mont., in 1924*

Yield per plant	Number of rows					
	Bozeman			Havre		
	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Hard Federation	Marquis
0.5 gram				3		3
1.5 grams				197	12	8
2.5 grams	4			69	3	6
3.5 grams	36	6	4	23	1	
4.5 grams	81	5	2	7	2	
5.5 grams	56	2	4			
6.5 grams	36		3			
7.5 grams	10					
8.5 grams	1					
9.5 grams						
Total	224	13	13	299	18	17
Average yield in grams	5.03	4.19	4.96	1.94	2.11	1.68

The plant data from Bozeman show that the hybrids averaged slightly more in yield than Marquis, the higher yielding parent. At Havre the hybrids were intermediate in yield, averaging less than Hard Federation, the higher yielding parent. Under the unfavorable droughty conditions prevailing at Havre the Hard Federation checks consistently outyielded the Marquis checks in 1924, while at Bozeman under favorable conditions the Marquis checks outyielded those of Hard Federation.

The F_3 yield data from Bozeman were affected by the premature ripening of some plants, due to root-rot. The Marquis parent was less affected by this disease than the hybrids or Hard Federation. The percentage of Marquis plants prematurely ripened was 13.6, that of Hard Federation 18.7, and that of the F_3 hybrids 18.0. There was considerable variation among the hybrid rows as to the extent of injury. Only one row, however, was not affected, the greatest amount of injury being 38 per cent. The F_3 hybrid material offered an opportunity to select both for resistance to the root-rot and for high yield.

Selections were made in the F_2 generation on a plant-yield basis. Some of the highest yielding F_2 plants were included among the families studied on the individual-plant basis in the F_3 generation. The highest and lowest yielding of the F_3 families, compared with the nearest labeled parent check rows, are given in Table 44.

Strain A3–90 was the lowest yielding of 25 strains at Bozeman and B1–78 the lowest of 16 strains at Havre. As an average for both points, strain B2–98 ranked lowest, although it outyielded Marquis, the lower yielding parent at Havre. No one strain had a yield significantly less than that of the lowest yielding parent at either of the two stations.

TABLE 44.—*Yield of individual F_3 plants from low and high yielding strains of Marquis–Hard Federation wheat crosses, in comparison with the parents, grown at Bozeman and Havre, Mont., in 1924*

Yield per plant	Bozeman strain and row Nos.						Havre strain and row Nos.					
	Low yielding			High yielding			Low yielding			High yielding		
	A3–90; 223	B2–98; 227	Hard Federation; 220	A1–24; 8	B1–65; 113	Marquis; 10	B1–78; 26	B2–98; 103	Marquis; 10	B1–65; 203	B1–47; 316	Hard Federation; 300
0.5 gram	7	6	4	1	3		30	8	31	2	3	4
1.5 grams	10	7	5	7	3	6	16	25	33	2	11	21
2.5 grams	11	10	14	1	6	12	1	26	1	15	9	21
3.5 grams	11	11	11	5	4	8		6		9	11	3
4.5 grams	10	7	14	3	8	12				9	1	3
5.5 grams	7	6	6	6	9	10					4	
6.5 grams	4	7	3	5	3	4				2		
7.5 grams	2	4	4	3	3	3						
8.5 grams			1	2	6	2						
9.5 grams	1			4	3	3						
10.5 grams			2	4	1	1						
11.5 grams		1		2	2							
12.5 grams				1	1	1						
13.5 grams				2	3							
14.5 grams				1	1							
15.5 grams												
16.5 grams												
17.5 grams												
18.5 grams				1								
Total	63	59	64	48	56	62	47	65	65	39	39	52
Average yield in grams	3.5	3.9	4.0	6.8	6.1	4.7	.9	2.0	1.0	3.2	2.7	2.1

Among the high-yielding strains A1–24 was first at Bozeman and B1–65 first at Havre. The latter strain also gave a high yield at Bozeman. It outyielded the higher yielding parent at both points. The mean yields and differences of this strain and the high-yielding parent at each point are as follows:

	Yield per plant (grams)
Bozeman:	
B1–65	6.07±0.32
Marquis	4.72± .21
Difference	1.35± .38
Havre:	
B1–65	3.24±0.14
Hard Federation	2.12± .09
Difference	1.12± .17

The differences are both significant. The parent plant in the F_2 generation yielded 11 grams and was one of those of highest yield. It appears therefore that from a high-yielding F_2 plant an F_3 strain has been obtained which gives promise of being significantly higher in yield than either parent when grown under conditions where each parent is best adapted. Other strains also have been obtained which are similarly promising.

The frequency distribution of the yields of all F_3 plants studied and those from duplicate parent check rows are given in Table 45, and the Bozeman data are shown graphically in Figure 9.

TABLE 45.—*Yields of 2,112 F_3 plants of Marquis–Hard Federation wheat crosses, in comparison with the parents, grown at Bozeman and Havre, Mont., in 1924*

Yield per plant	Bozeman			Havre		
	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Hard Federation	Marquis
0.5 gram	91	11	8	168	29	39
1.5 grams	173	13	15	289	56	59
2.5 grams	150	25	20	182	25	17
3.5 grams	172	23	16	59	4	8
4.5 grams	187	21	20	19	3	1
5.5 grams	131	9	17	5		1
6.5 grams	127	9	5	3		
7.5 grams	103	9	6			
8.5 grams	67	3	3			
9.5 grams	52	1	3			
10.5 grams	48	2	2			
11.5 grams	30					
12.5 grams	23		1			
13.5 grams	14					
14.5 grams	11					
15.5 grams	2					
16.5 grams	1					
17.5 grams	2					
18.5 grams	2					
19.5 grams	1					
Total	1,387	126	116	725	117	125
Average yield in grams	5.14	3.92	4.15	1.81	1.61	1.51

The data show that at both stations the average yield of the hybrid plants exceeded that of the parent varieties. This accords with the Bozeman F_2 data. It therefore appears that transgressive segregation has occurred for higher yielding hybrid plants than those of either the Hard Federation or Marquis parents.

CRUDE-PROTEIN CONTENT

The crude-protein content of wheat is a quality factor which in recent years is receiving increasing attention and is reflected in the price of the grain when marketed. It varies with environment and yield, but in part is controlled by factors associated with variety.

Lyon (*12*) and Roberts (*15*) have studied the variation and inheritance of crude-protein content within different plants and pure-line strains of a variety. The present study was designed to determine how the varietal factors which determine crude-protein content are inherited in hybrids.

The crude-protein content of the grain from F_2 and F_3 generations and parent plants and the bulk grain from nursery rows of F_3 strains and parents was determined.[3] Data on F_2 plants were obtained only from Bozeman material. Because of limited quantities of grain from single plants, single determinations were made on whole-wheat samples. The data are given in Table 46 and are shown graphically in Figure 11.

[3] The crude-protein determinations were made in the research laboratory of the grain division of the Bureau of Agricultural Economics. The work was all done under the direction of D. A. Coleman, in charge of the laboratory. The writers wish to express their appreciation to the officials of the Bureau of Agricultural Economics and of the grain division of the bureau, and particularly to Doctor Coleman, for the many courtesies extended in this cooperation. The writers wish also to express their appreciation to H. C. Fellows, who with Doctor Coleman made the determinations on the F_2 material, and to J. C. Wangler, junior biochemist, Bureau of Plant Industry, who made the determinations of the F_3 generation.

TABLE 46.—*Segregation in the F_2 generation into frequency classes for crude-protien content of the grain of 567 F_2 plants of Marquis–Hard Federation and reciprocal wheat crosses, in comparison with 189 plants of the parent varieties, grown at Bozeman, Mont., in 1923*

Crude-protein content (N×5.7, 13.5 per cent moisture)	F_2 hybrids			Hard Federation	Marquis
	Hard Federation × Marquis	Marquis× Hard Federation	Total		
12 per cent	1		1		
12.5 per cent		8	8	2	1
13 per cent	8	19	27	11	1
13.5 per cent	35	39	74	21	6
14 per cent	64	57	121	31	8
14.5 per cent	88	80	168	17	19
15 per cent	58	60	118	5	31
15.5 per cent	23	15	38	4	14
16 per cent	4	4	8	2	12
16.5 per cent		2	2		3
17 per cent	1		1		1
17.5 per cent					
18 per cent		1	1		
Total	282	285	567	93	96
Mean per cent and probable error	14.43±.03	14.31±.03	14.37±.02	13.99±.05	14.94±.06

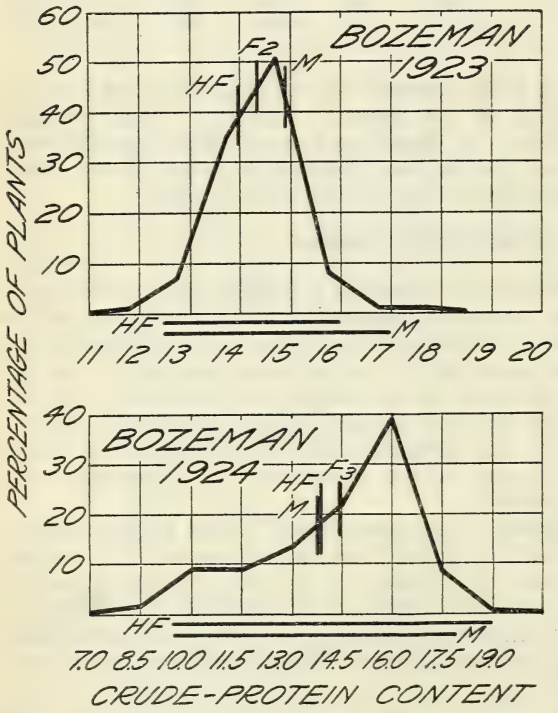

FIG. 11.—Frequency distribution of F_2 and F_3 hybrid wheat plants and the range of variation of the Marquis and Hard Federation parents, together with their average crude-protein content at Bozeman, Mont., in 1923 and 1924

The data show that in the F_2 generation the hybrids were intermediate to the parents in crude-protein content. The average of Marquis exceeded the average of Hard Federation by 0.95 ± 0.08 per cent. This difference is significant. The difference between the average of all the hybrids and that of Hard Federation, 0.38 ± 0.05 per cent, proves that the hybrids are significantly higher in crude-protein content than the Hard Federation parent. The difference between the average of the hybrids and that of Marquis, 0.57 ± 0.06 per cent, likewise proves that the hybrids are significantly lower in crude-protein content than the Marquis parent. The results from the reciprocal crosses differ by 0.12 ± 0.04 per cent in favor of the Hard Federation–Marquis crosses. This difference is statistically significant, although the difference of the

average of the reciprocal crosses from the average of the total hybrid population in each case is 0.06 ± 0.04, indicating but little, if any, paternal influence.

The variability of the hybrids in comparison with the parents, as indicated by coefficients of variability, is as follows:

	Coefficient of variation
F_2 hybrids	5.108 ± 0.102
Hard Federation	$5.081 \pm .251$
Marquis	$5.398 \pm .263$

The data show that the F_2 hybrids are slightly more variable in crude-protein content than Hard Federation and that Marquis is slightly but not significantly more variable in crude-protein content than either the hybrids or Hard Federation.

In 1924, at Bozeman, Moccasin, and Havre, bulk grain from nursery rows of F_3 strains and parent checks from the three stations was analyzed in duplicate for crude-protein content. Grain from the poorer yielding rows at Moccasin was not saved. The grain from all but one of each of the parent check rows also was discarded, so complete results from that station were not obtained. The frequency data in half per cent frequency classes are given in Table 47 and are shown graphically in Figure 12.

Figure 12 shows that the crude-protein content increases at the stations in their order at Moccasin, Bozeman, and Havre, this being the reverse order for the stations as to yield.

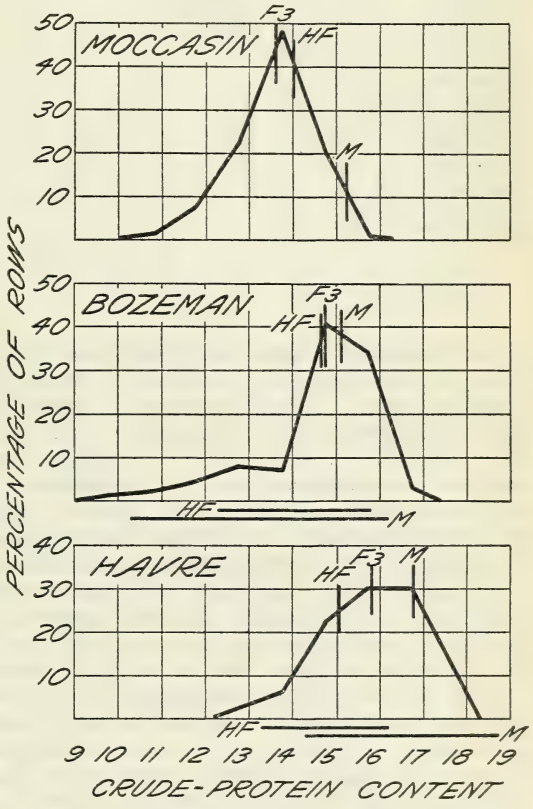

FIG. 12.—Frequency distribution of F_3 hybrid wheat strains and the range of variation of the Marquis and Hard Federation parent checks, together with their average crude-protein content at Moccasin, Bozeman, and Havre, Mont., in 1924

The Bozeman F_3 data show that the hybrids and also the Marquis parent are extremely variable. This is partly the result of soil variation. Two sections in the nursery, comprising about 15 rows each, were much lower in crude-protein content of the grain produced than the remainder of the nursery. Probably a lack of available nitrates in the soil of these two sections resulted in "yellow-berry" wheat with a lower crude-protein content. At this station the F_3 hybrids averaged practically the same as Hard Federation in crude-protein content and 0.4 per cent less than Marquis.

TABLE 47.—*Crude-protein content in the F_3 generation of grain from 639 strains of Marquis–Hard Federation wheat hybrids in comparison with 63 parent checks grown at Bozeman, Moccasin, and Havre, Mont., in 1924*

Crude-protein content	Bozeman			Moccasin			Havre		
	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Hard Federation	Marquis
9 per cent									
9.5 per cent	1								
10 per cent	1		1						
10.5 per cent	3								
11 per cent	2			1					
11.5 per cent	5		1	4					
12 per cent	5			5					
12.5 per cent	14			5			1		
13 per cent	4	2		21			7		
13.5 per cent	6			30			7	1	
14 per cent	9		1	27	1		11	3	
14.5 per cent	23	3		17			26	2	1
15 per cent	68	5	1	7		1	40	2	1
15.5 per cent	41	3	1	1			40	7	
16. per cent	35		4				49	3	2
16.5 per cent	7		4				51		4
17 per cent							37		4
17.5 per cent							20		2
18 per cent							8		2
18.5 per cent									1
Total	224	13	13	118	1	1	297	18	17
Average per cent	14.68	14.69	15.08	13.58	14.0	15.2	15.82	15.06	16.76

At Moccasin, where the yields were slightly higher than at Bozeman, the crude-protein contents of both hybrids and parents are slightly lower. The data from a single check row of each parent shows a difference of 1.2 per cent in favor of Marquis. Considering the variability shown in the Bozeman data it is likely that the relative percentages of the two parents are not correct and that this difference between the two is greater than actually existed. The F_3 hybrids averaged lower than Hard Federation, which in part may be caused by the lower yielding strains having been discarded.

At Havre, where the yields were low in comparison with those from Bozeman and Moccasin, the crude-protein content was higher. The average of the hybrids was nearly intermediate to that of the parents at this point, which is similar to the F_2 results at Bozeman.

The data on the crude-protein content of the grain of F_2 plants afforded opportunity to select for high crude-protein content in that generation. Some of the F_2 plants of highest crude protein were the parents of families studied on a plant basis in the F_3 generation. Data for some of the F_3 strains of highest and lowest average crude-protein content, compared with the nearest check rows of the parents studied in the same manner, are given in Table 48.

TABLE 48.—*Crude-protein content of grain from individual F_3 plants of low and high protein strains of Marquis–Hard Federation wheat crosses, in comparison with the parents, grown at Bozeman and Havre, Mont., in 1924*

Crude-protein content (N ×5.7, 13.5 per cent moisture)	Bozeman strain and row Nos.						Havre strain and row Nos.					
	Low protein			High protein			Low protein			High protein		
	A1–24; 8	B3–84; 145	Hard Federation; 20	B1–24; 38	B1–65; 113	Marquis; 229	B1–65; 203	B3–84; 229	Hard Federation; 300	B1–78; 26	B2–100; 47	Marquis; 10
8.5 per cent		2										
9 per cent		2										
9.5 per cent	2	6	1									
10 per cent	2	7	1									
10.5 per cent	1	3	10									
11 per cent	4	1	3					1				
11.5 per cent	6	4	3				3					
12 per cent	3	2	4					2				
12.5 per cent	6	9	3			1	2	2				
13 per cent	7	1	2	3					1			
13.5 per cent	5	7	3	2		1	2	2	4			
14 per cent	1	2	4	3	1	1	5	1	7			
14.5 per cent	2	2	3	5		1	9	5	8			
15 per cent		1	1	10	5	2	8	7	10			
15.5 per cent		2		15	5	2	4	10	12			
16 per cent				6	11	2	2	2	1	1	2	1
16.5 per cent				4	5	7	1	2	1	5	8	3
17 per cent			3	1	7	4	1		1	3	12	5
17.5 per cent			3	1	1	10			1	6	9	16
18 per cent						3				3	5	11
18.5 per cent										2	1	2
19 per cent						1					1	
Total	39	51	44	50	35	35	37	34	46	20	38	38
Average per cent	12.2	11.7	12.8	15.2	16.0	16.5	14.4	14.7	14.9	17.3	17.2	17.5

The data show that the strains of low crude-protein content are more variable than those of high crude-protein content. Strain B3–84 was the strain of lowest crude-protein content at Bozeman and second at Havre. At Bozeman it averaged significantly lower than Hard Federation, but not at Havre. The parent plant of this strain in the F_2 generation was one of the lowest in crude-protein content, with 13.7 per cent. Strains A1–24 at Bozeman and B1–65 at Havre, other F_3 families low in crude protein, were practically the same as Hard Federation. The F_2 parents of these strains were both medium in crude-protein content among the 567 plants studied for crude protein in this generation.

The three F_3 strains of high crude protein, B1–78, B1–65, and B2–100, are progeny of F_2 plants which had 16.7, 14.7, and 14.2 per cent crude protein, respectively. The average crude-protein content of Marquis was 14.9 per cent and of Hard Federation 14 per cent. In the F_3 generation at Bozeman strain B1–65 was highest in crude protein, with 16 per cent, whereas it was the lowest at Havre, with 14.4 per cent. This indicates the important part played by environment in determining quality factors. At Havre strains B1–78 and B2–100 were highest in crude protein, but neither exceeded, although they practically equaled, Marquis.

The F_2 parent plant of strain B1–24 was the highest in that generation, with a crude-protein content of 18.1 per cent, but the progeny in F_3 did not rank highest at either Bozeman or Havre. Data for this strain from Bozeman included in Table 49 show that it averaged 15.2 per cent crude protein, which was fairly high for that station.

At Havre 41 plants of it averaged but 15.1 per cent, which was not high in comparison with other strains and Marquis checks.

The data on individual plants of F_3 families do not show that transgressive segregation has been obtained for higher crude-protein strains than the Marquis parent, though at Bozeman one strain was obtained which had a significantly lower crude-protein content than Hard Federation.

Many F_3 strains which are significantly different in crude-protein content have been obtained, differing on the average by as much as 4.3 per cent at Bozeman and 2.9 per cent at Havre. The differences of numerous strains are from 5 to 10 times their probable errors.

Besides certain F_3 families studied for crude protein in individual plants, selections of promising plants were made in additional families and analyzed for crude-protein content. The frequency results obtained from all individual F_3 plants and parents at the three stations are presented in Table 49, and the Bozeman data are shown graphically in Figure 11.

TABLE 49.—*Crude-protein content of grain from 1,619 F_3 plants of Marquis–Hard Federation wheat crosses and 342 parent plants grown at Bozeman, Moccasin, and Havre, Mont., in 1924*

Crude-protein content	Number of plants						
	Bozeman			Moccasin	Havre		
	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	F_3 hybrids	Hard Federation	Marquis
8 per cent							
8.5 per cent	3						
9 per cent	6						
9.5 per cent	18	1	3				
10 per cent	21	2	5	1			
10.5 per cent	27	10	4	2			
11 per cent	23	3	4	3	1		
11.5 per cent	16	3	12	6	4		
12 per cent	25	4	9	17	2		
12.5 per cent	34	4	5	25	6		
13 per cent	34	4	3	60	7	1	1
13.5 per cent	33	3	1	53	20	4	
14 per cent	40	8	1	55	40	7	
14.5 per cent	43	8	3	45	50	9	1
15 per cent	80	4	3	24	62	13	3
15.5 per cent	108	5	2	6	83	22	4
16 per cent	117	8	2		61	13	6
16.5 per cent	70	4	7		74	15	12
17 per cent	49	4	4		56	3	18
17.5 per cent	12	3	10		47	2	23
18 per cent	5	1	3		27	1	18
18.5 per cent	1		1		15		4
19 per cent			1		2		
Total	765	79	83	297	557	90	90
Average per cent	14.42	13.80	13.75	13.54	15.78	15.46	17.06

The Bozeman data show that the selected F_3 plants averaged slightly more than individual plants from two extremely variable check rows of both parents. At Moccasin the hybrid F_3 plants averaged less than single tests of the parents grown in check rows, as shown in Table 49. The variability of the hybrids at Moccasin is about one-half that at Bozeman. At Havre the F_3 hybrids are intermediate between the parents but average nearer the lower protein Hard Federation parent. The hybrids, partly on account of greater numbers, appear more variable than the parents, exceeding them

principally in the lower percentages. The data as a whole indicate that crude-protein content is inherited in intermediate degrees between the parents, through multiple factors. There is little or no evidence to show that transgressive segregation has occurred for higher protein strains than Marquis. Because of the fact that high crude-protein F_3 strains were found less variable than low crude-protein strains and the Marquis parent, it is hoped that selection of high crude-protein F_3 plants may result in more uniform F_4 strains than Marquis and approach or equal it in average crude-protein content.

COMBINED CHARACTERS

No linkage was found between the four morphological characters—dwarfness, awnedness, and glume and kernel color—when the data on segregation were studied together.

The four quantitative characters—heading period, ripening period, fruiting period, and height—which were studied to determine their effect on yield and crude-protein content, are more or less associated, and the nature and amount are determined by the correlation studies which follow.

TABLE 50.—*Average yield per plant×crude-protein content in the F_3 generation of 521 Marquis–Hard Federation wheat hybrids, in comparison with 61 parent checks, in percentages of the average of Marquis at Bozeman and Havre, Mont., in 1924*

Yield×crude protein in percentages of the Marquis checks	Bozeman			Havre		
	F_3 hybrids	Hard Federation	Marquis	F_3 hybrids	Marquis	Hard Federation
230 per cent				2		
220 per cent						
210 per cent						1
200 per cent				1		
190 per cent				4		1
180 per cent				2		
170 per cent	1			5		
160 per cent	2			9		1
150 per cent	3		1	9	1	
140 per cent	8		1	9	2	
130 per cent	21		2	12	1	
120 per cent	14		1	23	2	1
110 per cent	32		1	29	2	2
100 per cent	34	2	1	49	1	2
90 per cent	42	3	1	58	1	3
80 per cent	29	4		48	3	4
70 per cent	18	2	4	28	1	2
60 per cent	10	2		8	3	1
50 per cent	7		1	1		
40 per cent	2					
30 per cent	1					
Total	224	13	13	297	17	18
Average per cent [1]	96.4	81.9	100.0	106.1	100.0	106.4

[1] Actual.

Yield and crude-protein content so far have been considered independently of each other. From an agronomic standpoint high yield is the end result of an improvement program. The senior writer (*5*) has held that high yield "is not the only consideration; the quality of the product is of equal importance to that of yield." On this hypothesis the F_3 hybrids and parents have been studied on the basis of the product of yield per plant and crude-protein content.

These products have been computed to a percentage basis with the average of all the Marquis parent check rows as 100 per cent. At Bozeman, Marquis gave the best results; at Havre, Hard Federation. Frequency data for the nursery-row results at the Bozeman and Havre stations are given in Table 50.

The data in Table 50 show that for combined yield and crude-protein content the hybrids average between the parents, but are nearer Marquis, the better parent at Bozeman, and nearer Hard Federation, the better parent at Havre.

At both stations the best check rows of the parents are exceeded by a few hybrid strains. At Bozeman approximately 35 per cent of the hybrids average better than 100 per cent, the average of Marquis, and 3 strains, or 1 per cent of the hybrids, exceed the best Marquis check row. At Havre nearly 35 per cent of the hybrids exceed 100, the average of Marquis, 23 strains exceed the best check row of that parent, and 2 strains exceed the best check row of Hard Federation.

The leading half-dozen hybrid strains at Bozeman, Moccasin, and Havre, ranked in order of the product of yield and crude-protein content, in comparison with the average of Marquis checks as 100 per cent, are shown in Table 51, together with their date of first heading, date of last ripening, fruiting period, height, yield, and crude-protein content.

The F_3 strains shown in Table 51 as the best for combined yield and crude-protein content are not any of those strains previously studied on a plant basis. This illustrates the necessity of giving careful consideration to more than a single character and shows that several years' results are necessary to determine the best strains for all factors concerned.

Only one strain, B1–57, ranked among the best six strains at both Bozeman and Havre. It ranked second at Bozemen and fifth at Havre and exceeded the best check row of Marquis by 10.6 per cent at Bozeman and 43 per cent at Havre. The greatest improvement appears to have resulted at Havre, where the six leading strains exceeded the average of Marquis check rows from 91.6 to 130.8 per cent and the best Marquis check from 42.6 to 81.8 per cent. At Bozeman, where the improvement was next in importance, the six leading strains exceeded the average of Marquis check rows from 48.6 to 75.4 per cent and the best Marquis check from 1.5 to 28.3 per cent. At Moccasin, where improvement was least pronounced, the yields were the largest and were computed only on an acre basis. This resulted in a disadvantage for the hybrids in comparison with the parents, because the dwarf plants reduced the yields. However, the six best strains were from 7.7 to 25.2 per cent better than the average of the Marquis checks.

At the three stations most of these best strains are earlier in heading than Marquis and later in ripening than Hard Federation. None are earlier heading than Hard Federation, but several are later ripening than Marquis. All but two of the strains have as long or longer fruiting periods than the average of Hard Federation, and all but four are as tall or taller than the average of Marquis. This indicates that improvement in yield and crude-protein content has been obtained in hybrids by combining the advantages of the long fruiting period of Hard Federation and the height of Marquis.

TABLE 51.—*Leading F_3 strains at Bozeman, Moccasin, and Havre, as determined by the product of their yield and crude-protein content together with other characters, in comparison with the best and average parent checks*

Station and strain	Row No.	Combined characters							
		Date of—		Fruiting period (days)	Height (inches)	Yield per plant (grams)	Crude-protein content (per cent)	Yield×crude protein	
		First heading	Last ripening					Product	Percentage of the average of Marquis
Bozeman:									
B1-102	138	July 8	Sept. 4	58	40	8.9	15.1	134.39	175.4
B1-57	136	July 6	Sept. 3	59	38	8.0	15.1	120.80	157.7
B3-53	117	July 5	Sept. 2	59	37	7.9	15.1	119.29	155.7
A2-47	77	---do---	Sept. 1	58	37	8.0	14.6	116.80	152.5
B2-57	115	---do---	Sept. 3	60	34	7.4	15.4	113.96	148.8
B2-37	39	July 9	Sept. 4	57	39	7.3	15.6	113.88	148.6
Best Marquis	250	July 10	Sept. 3	55	37	7.0	16.1	112.70	147.1
Best Hard Federation	120	July 3	Aug. 29	57	29	5.2	14.8	76.96	100.5
Average Marquis	------	July 9	Sept. 2	55	38	5.0	15.1	[1] 76.61	100.0
Average Hard Federation	------	July 4	Aug. 30	57	29	4.2	14.7	[1] 62.76	81.9
Moccasin:									
A1-30	37	July 5	Aug. 20	46	45	[2] 44.4	13.2	586.08	125.2
C1-23	68	July 8	Aug. 22	45	43	38.0	14.1	535.80	114.4
C1-21	67	July 5	Aug. 21	47	44	39.4	13.5	531.90	113.6
A2-91	166	July 7	Aug. 22	46	44	37.0	14.2	525.40	112.2
A2-52	121	July 4	Aug. 17	44	42	36.7	13.8	506.46	108.2
A3-47	6	July 7	Aug. 18	42	45	36.8	13.7	504.16	107.7
Best Marquis	70	July 9	Aug. 24	46	43	34.7	--------	--------	--------
Best Hard Federation	40	July 3	Aug. 19	47	41	39.3	--------	--------	--------
Average Marquis	------	July 9	Aug. 23	45	43	30.8	[3] 15.2	468.16	100.0
Average Hard Federation	------	July 3	Aug. 17	45	40	29.7	[3] 14.0	415.80	88.8
Havre:									
B1-51	318	July 11	Aug. 20	40	30	4.8	14.2	68.16	230.8
B1-54	319	July 10	Aug. 21	42	25	4.4	15.4	67.76	229.5
B2-89	324	---do---	---do---	42	28	4.3	13.6	58.48	198.0
B1-48	317	July 11	Aug. 19	39	28	4.4	13.1	57.64	195.2
B1-57	321	---do---	Aug. 21	41	30	4.2	13.5	56.70	192.0
B1-19	201	July 10	Aug. 20	41	28	4.1	13.8	56.58	191.6
Best Hard Federation	335	July 8	Aug. 21	44	26	4.2	14.7	61.74	209.1
Best Marquis	310	July 12	Aug. 20	39	27	2.7	16.3	44.01	149.0
Average Hard Federation	------	July 8	Aug. 16	39	22	2.1	15.1	[1] 31.43	106.4
Average Marquis	------	July 13	Aug. 19	37	23	1.7	16.8	[1] 29.53	100.0

[1] Average of the products of the individual check rows.
[2] Yields at Moccasin are in bushels per acre.
[3] Crude-protein content based on only one row.

CORRELATION OF CHARACTERS IN THE F_2 AND F_3 GENERATIONS

The inheritance of the six quantitative characters previously discussed is further studied in connection with their correlation under different environmental conditions. The amount of correlation between the different characters serves as a guide for making selections. Correlation coefficients have been determined for all of the possible combinations of the six characters—heading period, ripening period, fruiting period, height, yield, and crude-protein content. The correlations were made on differing amounts of material grown at the three Montana stations—Bozeman, Moccasin, and Havre—during one or both of the two years 1923 and 1924. In 1923 the correlations were based on results from individual F_2 plants. In 1924 the correlations were obtained on the row data from F_3 strains.

The correlated inheritance of a character, one year with another, was found for all characters at Bozeman and for some at Moccasin. Also the correlation of each character at Bozeman one year with that from Havre the next year was determined to learn the environmental effect, as conditions at the two stations are very different.

The weighted averages of the coefficients obtained at the different stations or in different years also have been determined and serve to show the trend of correlation under Montana conditions. Probable errors for these averages have not been determined, as four observations are not sufficient for applying the probable-error concept. More observations are necessary before the significance of average correlations may be determined.

HEADING PERIOD

The coefficients of correlation obtained for the heading period one year with another at Bozeman and at Bozeman one year with Havre the next year are shown in the first portion of Table 52. The coefficients obtained for heading period with ripening period, fruiting period, height, yield, and crude-protein content follow in the order listed.

TABLE 52.—*Correlation coefficients and probable errors of heading period in F_2 and F_3 generations and of heading period with ripening period, fruiting period, height, yield, and crude-protein content of Marquis-Hard Federation wheat crosses grown at Bozeman, Moccasin, and Havre, Mont., in one or both of the years 1923 and 1924*

Heading period	Correlated with—		Number of F_2 plants or F_3 strains	Correlation coefficient and probable error
F_2, Bozeman, 1923	Heading period	F_3, Bozeman, 1924	224	0.505±0.034
		F_3, Havre, 1924	300	.580± .026
Total or average			524	.548
F_2, Bozeman, 1923	Ripening period	F_2, Bozeman, 1923	583	.333± .025
F_3, Bozeman, 1924		F_3, Bozeman, 1924	224	.387± .038
F_3, Moccasin, 1924		F_3, Moccasin, 1924	150	.639± .033
F_3, Havre, 1924		F_3, Havre, 1924	298	.422± .032
Total or average			1,255	.400
F_2, Bozeman, 1923	Fruiting period	F_2, Bozeman, 1923	583	−.249± .026
F_3, Bozeman, 1924		F_3, Bozeman, 1924	224	−.307± .041
F_3, Moccasin, 1924		F_3, Moccasin, 1924	150	−.161± .054
F_3, Havre, 1924		F_3, Havre, 1924	298	−.362± .034
Total or average			1,255	−.276
F_2, Bozeman, 1923	Height	F_2, Bozeman, 1923	583	.090± .028
F_3, Bozeman, 1924		F_3, Bozeman, 1924	224	.336± .040
F_3, Moccasin, 1924		F_3, Moccasin, 1924	150	.006± .055
F_3, Havre, 1924		F_3, Havre, 1924	299	.128± .038
Total or average			1,256	.133
F_2, Bozeman, 1923	Yield	F_2, Bozeman, 1923	583	−.042± .028
F_3, Bozeman, 1924		F_3, Bozeman, 1924	224	.106± .045
F_3, Moccasin, 1924		F_3, Moccasin, 1924	150	.157± .054
F_3, Havre, 1924		F_3, Havre, 1924	299	−.028± .039
Total or average			1,256	.011
F_2, Bozeman, 1923	Crude protein	F_2, Bozeman, 1923	567	.051± .028
F_3, Bozeman, 1924		F_3, Bozeman, 1924	224	.072± .045
F_3, Moccasin, 1924		F_3, Moccasin, 1924	118	−.080± .062
F_3, Havre, 1924		F_3, Havre, 1924	297	.183± .038
Total or average			1,206	.073

The data show that the heading period in one year is correlated with that in another year to a high positive degree both at the same station and at different stations. The average coefficient of 0.548 may be considered very important. The correlation between F_2 plants in 1923 and F_3 strains in 1924 at Bozeman illustrates the nature of the inheritance, and the data are given in Table 53.

TABLE 53.—*Correlation of heading period between F_2 plants and F_3 strains in Marquis–Hard Federation wheat crosses grown at Bozeman, Mont., in 1923 and 1924*

Dates of heading, 1924	Dates of heading, July, 1923							
	14	16	18	20	22	24	26	Total
July 3	1	1						2
July 4	15	15	9					39
July 5	16	22	22	5	1			66
July 6	5	22	24	3	2			56
July 7	1	11	20	7	1			40
July 8		1	8	4	2	1		16
July 9			1	1			1	3
July 10		1						1
July 11						1		1
Total	38	73	84	20	6	2	1	224

$r = 0.505 \pm 0.034$.

Significant positive correlations were obtained between heading period and ripening period. The average correlation of 0.400 is important, since the characters are independent in chance of occurence but dependent in degrees of effect.

Significant negative correlations were obtained between heading period and fruiting period. The average correlation of -0.276 may be considered of some importance, although not so high as might be expected of characters dependent in chance of occurrence and with partial association. The correlation between the two characters in F_2 plants grown at Bozeman in 1923 is representative of the average results, and the data are given in Table 54.

TABLE 54.—*Correlation between heading period and fruiting period in F_2 plants of Marquis–Hard Federation wheat crosses grown at Bozeman, Mont., in 1923*

Heading period	Fruiting period (days)							
	35	38	41	44	47	50	53	Total
July 14			6	14	11	25	2	58
July 16		7	30	48	72	47	3	207
July 18		10	58	47	88	22	3	228
July 20	1	1	14	33	12	5		66
July 22			2	8	3	2		15
July 24			4	1	2			7
July 26		1		1				2
Total	1	19	114	152	188	101	8	583

$r = -0.249 \pm 0.026$

Heading period and height were found to be positively correlated, the later heading strains being the taller. Only two of the four correlations, however, were significant, and the average correlation of 0.133 can not be considered very important.

Little or no correlation was found between heading period and yield. The results in two instances were negative, in two positive, and in no case significant. The average correlation was only 0.011.

Only at Havre under severe drought conditions was there found to be a significant correlation between heading period and crude-protein content. There the later heading strains were found to have a greater crude-protein content. Under the favorable conditions at Bozeman small positive correlations were obtained, but at Moccasin the results were negative. The average correlation of 0.073 is not important.

RIPENING PERIOD

The coefficients of correlation obtained for the ripening period one year with another at both Bozeman and Moccasin and at Bozeman one year with Havre the next year are given in the first portion of Table 55. Following are the coefficients obtained for ripening period with fruiting period, height, yield, and crude-protein content.

TABLE 55.—*Correlation coefficients and probable errors of the ripening period in F_2 and F_3 generations and of ripening period with fruiting period, height, yield, and crude-protein content of Marquis–Hard Federation wheat crosses grown at Bozeman, Moccasin, and Havre, Mont., in one or both of the years 1923 and 1924*

Ripening period	Correlated with—		Number of F_2 plants or F_3 strains	Correlation coefficient and probable error
F_2, Bozeman, 1923	Ripening period	F_3, Bozeman, 1924	224	0.372±0.039
F_2, Moccasin, 1923		F_3, Moccasin, 1924	150	−.064± .055
F_2, Bozeman, 1923		F_3, Havre, 1924	298	.051± .039
Total or average			672	.132
F_2, Bozeman, 1923	Fruiting period	F_2, Bozeman, 1923	583	.817± .009
F_3, Bozeman, 1924		F_3, Bozeman, 1924	224	.758± .019
F_3, Moccasin, 1924		F_3, Moccasin, 1924	150	.654± .032
F_3, Havre, 1924		F_3, Havre, 1924	298	.693± .020
Total or average			1,255	.758
F_2, Bozeman, 1923	Height	F_2, Bozeman, 1923	587	.134± .027
F_3, Bozeman, 1924		F_3, Bozeman, 1924	224	.372± .039
F_3, Moccasin, 1924		F_3, Moccasin, 1924	150	.196± .053
F_3, Havre, 1924		F_3, Havre, 1924	298	.525± .028
Total or average			1,259	.276
F_2, Bozeman, 1923	Yield	F_2, Bozeman, 1923	587	.275± .026
F_3, Bozeman, 1924		F_3, Bozeman, 1924	224	.337± .040
F_3, Moccasin, 1924		F_3, Moccasin, 1924	150	.177± .053
F_3, Havre, 1924		F_3, Havre, 1924	298	.565± .027
Total or average			1,259	.343
F_2, Bozeman, 1923	Crude protein	F_2, Bozeman, 1923	567	−.148± .028
F_3, Bozeman, 1924		F_3, Bozeman, 1924	224	.547± .032
F_3, Moccasin, 1924		F_3, Moccasin, 1924	118	.013± .062
F_3, Havre, 1924		F_3, Havre, 1924	296	−.378± .034
Total or average			1,205	−.060

The data show that the ripening period is less strongly inherited than the heading period. At Bozeman there was an important and significant positive correlation obtained, but at Moccasin the cor-

relation was slightly negative. The correlation between F_2 plants at Bozeman in 1923 and F_3 strains produced therefrom at Havre in 1924 was positive but small and not significant. The average correlation of 0.132 can not be considered very important.

The ripening period and the fruiting period are very strongly correlated, as shown by all of the four coefficients obtained. The average correlation of 0.758 is larger than between any other pair of characters and due to their dependence in chances of occurrence. The F_2 data at Bozeman illustrate how dependent each factor is on the other and are given in Table 56.

TABLE 56.—*Correlation between heading period and fruiting period in F_2 plants of Marquis–Hard Federation wheat crosses grown at Bozeman, Mont., in 1923*

Fruiting period	Ripening period (days)									Total
	August				September					
	25	27	29	31	2	4	6	8	10	
36 days	1									1
38 days	8				1					9
40 days	13	13	5		1					32
42 days	8	41	31	8	3	1				92
44 days		17	36	14	19		2			88
46 days		2	21	23	69	7	2			124
48 days				10	90	15	10	3		128
50 days				1	38	29	16	2		86
52 days					1	7	11	2	1	22
54 days								1		1
Total	30	73	93	56	222	59	41	8	1	583

$r = 0.817 \pm 0.009$.

The ripening period also is positively correlated with height, the later strains being the taller. Significant correlations were obtained in four instances, and the average correlation of 0.276 is fairly important.

A longer ripening period also was found to be positively correlated with larger yield. Under the widely different Montana conditions significant positive correlations were obtained in all four experiments, and the average correlation of 0.343 is important.

The ripening period and crude-protein content are on the average slightly negatively correlated. This relationship was obtained in two of four instances. In 1923 at Bozeman the F_2 results probably are the most typical of average conditions with a correlation coefficient of -0.148 ± 0.028. In 1924 at Bozeman two bad spots in the nursery, owing probably to a lack of available nitrates, resulted in earlier maturity of about 30 rows and "yellow-berry" kernels. This increased an otherwise positive correlation about twice the amount it might have been. At Moccasin in 1924 the correlation was practically zero. At Havre, however, under severe drought conditions the important negative correlation of -0.378 ± 0.034 was obtained. This illustrates the differences which are frequently obtained because of the lack of a proper balance between soil moisture and available nitrates.

FRUITING PERIOD

The coefficients of correlation obtained for the fruiting period one year with another at Bozeman and at Bozeman one year with Havre the next year are given in the first portion of Table 57 and are followed by the coefficients obtained for the fruiting period with height, yield, and crude-protein content.

TABLE 57.—*Correlation coefficients and probable errors of fruiting period in F_2 and F_3 generations and of fruiting period with height, yield, and crude-protein content of Marquis–Hard Federation wheat crosses grown at Bozeman, Moccasin, and Havre, Mont., in one or both of the years 1923 and 1924*

Fruiting period	Correlated with—		Number of F_2 plants or F_3 strains	Correlation coefficient and probable error
F_2, Bozeman, 1923	Fruiting period	F_3, Bozeman, 1924	224	0.097±0.045
		F_3, Havre, 1924	298	.000± .039
Total or average			522	.042
F_2, Bozeman, 1923	Height	F_2, Bozeman, 1923	583	.078± .028
F_3, Bozeman, 1924		F_3, Bozeman, 1924	224	.144± .044
F_3, Moccasin, 1924		F_3, Moccasin, 1924	150	.246± .052
F_3, Havre, 1924		F_3, Havre, 1924	298	.657± .022
Total or average			1,255	.247
F_2, Bozeman, 1923	Yield	F_2, Bozeman, 1923	583	.324± .025
F_3, Bozeman, 1924		F_3, Bozeman, 1924	224	.296± .041
F_3, Moccasin, 1924		F_3, Moccasin, 1924	150	.079± .055
F_3, Havre, 1924		F_3, Havre, 1924	298	.601± .025
Total or average			1,255	.355
F_2, Bozeman, 1923	Crude protein	F_2, Bozeman, 1923	567	−.170± .028
F_3, Bozeman, 1924		F_3, Bozeman, 1924	224	.512± .033
F_3, Moccasin, 1924		F_3, Moccasin, 1924	118	.082± .062
F_3, Havre, 1924		F_3, Havre, 1924	296	−.537± .028
Total or average			1,205	−.109

The data show that the fruiting period was not inherited to a significant degree at Bozeman one year with another and that at Bozeman one year with Havre the next a zero coefficient was obtained.

Fruiting period and height were found to be positively correlated with significant coefficients obtained for three of the four experiments. The average correlation of 0.247 is hardly important.

Fruiting period and yield were found positively correlated and in a significant amount in three of the four experiments. The average coefficient of 0.355 is much more important than that of either heading period or ripening period with yield. Of the five factors studied for their association with yield, fruiting period is second only to that of height. The important relation between fruiting period and yield is illustrated by the F_2 data from Bozeman in Table 58.

On the average, fruiting period was found to be negatively correlated with crude-protein content, although in two instances the correlations were positive. At Bozeman in the F_2 generation there resulted a fairly large and significant negative correlation and at Havre in F_3 a very large one. At Bozeman in the F_3 generation, however, a large positive correlation was obtained, and at Moccasin the coefficient was slightly positive. The average correlation of −0.109 is not important. This again illustrates, as in the case of

the ripening period, the environmental effect, due possibly to wide differences in the balance between soil moisture and available nitrates at the three stations.

TABLE 58.—*Correlation between fruiting period and yield in F_2 plants of Marquis–Hard Federation wheat crosses grown at Bozeman, Mont., in 1923*

Fruiting period	Yield per plant (grams)													
	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	Total
36 days		1												1
38 days		2	1	2	1		1		2					9
40 days			1	5	7	5	8	4	2					32
42 days	1		2	9	10	27	20	14	5	3	1			92
44 days				4	12	21	20	15	9	4	3			88
46 days		1	1	6	8	17	32	26	22	9	2			124
48 days			2	5	8	22	36	22	12	12	6	2	1	128
50 days			2	2	7	9	17	17	13	15	2	2		86
52 days					1	1	4	9	3	2	1		1	22
54 days										1				1
Total	1	4	9	33	54	102	138	107	68	46	15	4	2	583

$r=0.324\pm0.025$.

HEIGHT

The coefficients of correlation obtained for height one year with another at both Bozeman and Moccasin and at Bozeman one year with Havre the next year are given in the first portion of Table 59, followed by the coefficients obtained for height with yield and crude-protein content.

TABLE 59.—*Correlation coefficients and probable errors of height in F_2 and F_3 generations and of height with yield and crude-protein content of Marquis–Hard Federation wheat crosses grown at Bozeman, Moccasin, and Havre, Mont., in one or both of the years 1923 and 1924*

Height	Correlated with—		Number of F_2 plants or F_3 strains	Correlation coefficient and probable error
F_2, Bozeman, 1923	Height	F_3, Bozeman, 1924	224	0.485±0.034
		F_3, Havre, 1924	299	−.045± .039
F_2, Moccasin, 1923	Height	F_3, Moccasin, 1924	150	.317± .050
Total or average			673	.212
F_2, Bozeman, 1923	Yield	F_2, Bozeman, 1923	587	.360± .024
F_3, Bozeman, 1924		F_3, Bozeman, 1924	224	.381± .039
F_3, Moccasin, 1924		F_3, Moccasin, 1924	150	.230± .052
F_3, Havre, 1924		F_3, Havre, 1924	299	.798± .014
Total or average			1,260	.452
F_2, Bozeman, 1923	Crude protein	F_2, Bozeman, 1923	567	−.025± .028
F_3, Bozeman, 1924		F_3, Bozeman, 1924	224	.088± .045
F_3, Moccasin, 1924		F_3, Moccasin, 1924	118	.058± .062
F_3, Havre, 1924		F_3, Havre, 1924	297	−.737± .018
Total or average			1,206	−.171

The data show that height was positively correlated to a significant degree at both Bozeman and Moccasin one year with another, but that at Bozeman one year and Havre the next the correlation was practically zero. The Moccasin data which are given in Table 60 well illustrate the inheritance of factors for height and the amount of association which has been obtained one year with another at the same station.

TABLE 60.—*Correlation between height of F_2 plants and average height of F_3 strains of Marquis–Hard Federation wheat crosses grown at Moccasin, Mont., in 1923 and 1924*

Height of row, 1924	Height of plant, 1923 (inches)										
	28	30	32	34	36	38	40	42	44	46	Total
38 inches					2		1	1			4
39 inches	1		1	1		2	4	1			10
40 inches		1			2		2	1			6
41 inches				1	4	7	3	3			18
42 inches		1		1	6	9	8	3	2		30
43 inches		1	1	1	4	7	8	5	2		29
44 inches				4	3	3	6	8	7	3	34
45 inches						2	9	2	2		15
46 inches							1	3			4
Total	1	3	2	8	21	30	42	27	13	3	150

$r=0.317\pm0.050$.

Significant positive correlations were obtained in all instances between height and yield. The average correlation, 0.452, indicates the importance of environment in affecting both height and yield. Of the five factors here studied, height has given the highest coefficient of correlation with yield.

The Bozeman F_3 data are shown in Table 61 and represent the association of height and yield under favorable conditions. Under unfavorable conditions, such as at Havre, height and yield are more highly correlated.

TABLE 61.—*Correlation between height of F_3 strains and yield of Marquis–Hard Federation wheat crosses grown at Bozeman, Mont., in 1924*

Height of row	Average yield of plant (grams)							
	2.5	3.5	4.5	5.5	6.5	7.5	8.5	Total
28.5 inches		1	6					7
30.5 inches	2	3	14	4	2			25
32.5 inches	2	12	21	12	8			55
34.5 inches		12	23	22	9	2		68
36.5 inches		7	14	13	10	2		46
38.5 inches		1	3	5	5	6		20
40.5 inches					2		1	3
Total	4	36	81	56	36	10	1	224

$r=0.381\pm0.039$.

On the average, height was found to be negatively correlated with crude-protein content. In three out of four experiments, however, the correlations were small and not significant. Only at Havre, under droughty conditions and where height was very highly correlated with yield, was there an important negative correlation between height and crude-protein content.

YIELD

Coefficients of correlation obtained for yield one year with another at both Bozeman and Moccasin and at Bozeman one year with Havre the next year are given in the first half of Table 62, followed by those for yield with crude-protein content.

TABLE 62.—*Correlation coefficients and probable errors of yield in F_2 and F_3 generations and of yield with crude-protein content of Marquis–Hard Federation wheat crosses grown at Bozeman, Moccasin, and Havre, Mont., in one or both of the years 1923 and 1924*

Yield	Correlated with—	Number of F_2 plants or F_3 strains	Correlation coefficient and probable error
F_2, Bozeman, 1923	Yield—F_3, Bozeman, 1924	224	0.225±0.043
	Yield—F_3, Havre, 1924	299	.004± .039
F_2, Moccasin, 1923	Yield—F_3, Moccasin, 1924	150	.255± .051
Total or average		673	.134
F_2, Bozeman, 1923	Crude protein—F_2, Bozeman, 1923	567	−.231± .027
F_3, Bozeman, 1924	Crude protein—F_3, Bozeman, 1924	224	.256± .042
F_3, Moccasin, 1924	Crude protein—F_3, Moccasin, 1924	118	−.201± .060
F_3, Havre, 1924	Crude protein—F_3, Havre, 1924	297	−.732± .018
Total or average		1,206	−.261

The data show that yield was positively correlated to a significant degree at both Bozeman and Moccasin one year with another, but that there was practically a zero correlation between the yield at Bozeman one year with that of Havre the year following. This shows the necessity of making selections at the station at which the wheats are to be tested and in the section for which they are being developed. The inheritance of yield as measured in grams from F_2 plants with that of bushels per acre from F_3 strains at Moccasin is given in Table 63 and illustrates the amount of correlation which was obtained when F_2 plants were definitely spaced and favorable conditions were present in both years.

TABLE 63.—*Correlation between yield in grams of F_2 plants and the yield per acre in bushels of F_3 rows of Marquis–Hard Federation wheat crosses grown at Moccasin, Mont., in 1923 and 1924*

Acre yield of F_3 rows in 1924	Yield of F_2 plants, 1923 (grams)										Total
	2	5	8	11	14	17	20	23	26	29	
12.5 bushels				1	1						2
17.5 bushels		4	5	3							12
22.5 bushels	1	5	4	1	4	2	3				20
27.5 bushels		8	19	20	7	3	2	1		1	61
32.5 bushels	1	1	8	14	9	3		1	1	1	39
37.5 bushels			2	4	5	2	2				15
42.5 bushels						1					1
Total	2	18	38	43	26	11	7	2	1	2	150

$r=0.255\pm0.051$.

On the average, yield was found negatively correlated with crude-protein content. This relationship was found with F_2 plants grown at Bozeman and from F_3 strains grown at Moccasin and Havre. The F_3 strains at Bozeman, however, gave a positive correlation. The average correlation of -0.261 may or may not represent the usual association. Exceptions to this negative relationship are possible, as shown by the data from Bozeman which are given in Table 64. There conditions were favorable, causing high yields and heavyweight kernels having a small percentage of "yellow berry."

TABLE 64.—*Correlation between average yield per plant and crude-protein content of F_3 strains of Marquis–Hard Federation wheat crosses grown at Bozeman, Mont., in 1924*

Crude-protein content	Average yield of plant (grams)							Total
	2.5	3.5	4.5	5.5	6.5	7.5	8.5	
10 per cent		2						2
11 per cent		5						5
12 per cent	1	2	5	1	1			10
13 per cent	1	5	7	4	1			18
14 per cent		2	7	5	1			15
15 per cent	1	10	29	26	16	8	1	91
16 per cent	1	8	30	18	17	2		76
17 per cent		2	3	2				7
Total	4	36	81	56	36	10	1	224

$r=0.256\pm0.042$.

The other extreme condition, showing a large negative correlation, is illustrated by the Havre data and is given in Table 65. As previously mentioned, the season at Havre was very dry, and under such unfavorable conditions the yields were low and the kernels light in weight but hard and vitreous.

TABLE 65.—*Correlation between average yield per plant and crude-protein content of F_3 strains of Marquis–Hard Federation wheat crosses grown at Havre, Mont., in 1924*

Crude-protein content	Average yield per plant (grams)									Total
	0.8	1.3	1.8	2.3	2.8	3.3	3.8	4.3	4.8	
12.5 per cent								1		1
13 per cent						2	4	1		7
13.5 per cent				1		3	1	2		7
14 per cent			1	3	1	4		1	1	11
14.5 per cent			11	5	3	6	1			26
15 per cent		3	17	14	5	1				40
15.5 per cent		5	16	12	5	1		1		40
16 per cent		10	27	12						49
16.5 per cent		16	29	6						51
17 per cent	1	21	14	1						37
17.5 per cent	2	15	3							20
18 per cent		8								8
Total	3	78	118	54	14	17	6	6	1	297

$r=-0.732\pm0.018$.

The distribution of the data in Table 65 strikingly illustrates the negative relationship which exists between yield and crude-protein content under dry-farming conditions and shows the importance of giving equal consideration to factors for quality and factors for yield in an improvement program in wheat breeding.

CRUDE-PROTEIN CONTENT

The coefficients of correlation obtained for crude-protein content one year with another at Bozeman and Bozeman one year with Havre the year following are given in Table 66.

TABLE 66.—*Correlation coefficients and probable errors of crude-protein content in F_2 and F_3 generations of Marquis–Hard Federation wheat crosses grown at Bozeman and Havre, Mont., in one or both of the two years 1923 and 1924*

Crude protein	Correlated with—	Number of F_2 plants or F_3 strains	Correlation coefficient and probable error
F_2, Bozeman, 1923	Crude protein—F_3, Bozeman, 1924	221	0.097±0.045
	Crude protein—F_3, Havre, 1924	287	.093± .039
Total or average		508	.095

The coefficients obtained are positive but not significant. Under the conditions under which the crop was grown at Bozeman in both 1923 and 1924 and at Bozeman in 1923 and Havre in 1924 no evidence was obtained to show that the segregation for crude-protein content that occurred was inherited in an important amount.

SUMMARY

This inheritance and environmental study was made for the purpose of determining the factors for yield and quality of spring wheat on the dry lands of Montana.

Hard Federation was selected for crossing with Marquis, the most important commercial variety, because of several contrasting characters, principally the longer fruiting period of Hard Federation and the greater height of Marquis, which affect differently their adaptation in certain localities and seasons.

The material was studied at three points—Bozeman, under fairly humid conditions in the Gallatin Valley; Moccasin, under semiarid or average dry-land conditions in the Judith Basin; and Havre, under marginal dry farming conditions in the so-called triangle. Three distinct environmental conditions are thus represented.

Twelve F_1 families were studied in the F_2 generation. Six were grown at Bozeman and six at Moccasin. These were divided equally between reciprocal crosses at each station. No important maternal or paternal influence was found, although a few statistically significant differences were obtained.

Dwarf plants appeared in the F_2 generation in all F_1 families in a ratio close to 13 normals to 3 dwarfs. In F_3 the normals bred true or segregated in ratios of 13 normals to 3 dwarfs or 3 normals to 1 dwarf. The dwarfs segregated in the ratio of 3 dwarfs to 1 normal or bred true for dwarfs. The Bozeman F_2 data corrected on the basis of F_3 results gave a close fit to a 7 : 4 : 2 : 2 : 1 genotypic ratio for the above breeding groups. The results were satisfactorily explained on a 2-factor genetic basis by assuming DD a factor for dwarfs and NN an inhibitor or factor for normals.

The inheritance of awnedness was studied by grouping the material into the three following classes: (1) Awnless, (2) apically awnletted, (3) awnletted. In the F_2 generation the combined classes 1 and 2 compared with 3 were close to a 3 : 1 ratio. Class 1, in comparison with classes 2 and 3 combined, was close to a 1 : 15 ratio. In the F_3 generation, classes 1 and 3 bred true. The Moccasin F_2 data for the three classes were close to a 1 : 11 : 4 ratio, and the Bozeman F_2

data, corrected on the basis of F_3 results, also gave a close fit to that ratio. A 2-factor genetic interpretation of the results was made on the basis of primary (A, a) and secondary (B, b) factor pairs.

Brown glumes were dominant to white, and in the F_2 generation the deviations in numbers were not significantly different from the simple 3 : 1 ratio in any of the 12 F_1 families or in the several totals. In the F_3 generation the white-glumed plants all bred true and the brown-glumed plants either bred true or segregated in a 3 : 1 ratio in proportions which approximated the ratio of 1 : 2.

Red kernels were dominant to white, and in the F_2 generation 10 of the 12 F_1 families segregated in numbers close to a 2-factor 15 : 1 ratio and the two other families close to the single factor 3 : 1 ratio. In the F_3 studies of the 2-factor families the white-kerneled strains all bred true and the red-kerneled strains bred true or segregated in 3 : 1 or 15 : 1 ratios in proportions approximating a 7 : 4 : 4 ratio.

Maturity studies were made from the dates of heading, dates of ripening, and the days between these dates or from the heading, ripening, and fruiting periods.

In F_2 early heading was partially dominant, although there were no large early and no small late groups. The hybrids were significantly more variable than the parents. No earlier heading strains than Hard Federation were produced, but transgressive segregation for lateness of heading was found, as F_3 strains were obtained which were significantly later in heading than Marquis both at Bozeman and Havre.

The time of ripening of the hybrids was nearly intermediate between the parents and not significantly more variable. Strains as uniform as the parents for the ripening period were obtained in the F_3 generation, some of which were as late or later in ripening than the Marquis parent.

The average fruiting period of the hybrids was intermediate to those of the parents. Strains of short and long fruiting periods were observed which differed on the average by as much as 6.7 days at Bozeman and 8.1 days at Havre. One F_3 strain was obtained which was significantly shorter than that of Marquis at both stations, but no hybrids were found to have a longer fruiting period than that of Hard Federation.

From F_2 and F_3 studies, all gradations between the parents were found in average height without significantly greater variability than in the parents. The respective heights of the parents have been approximately reached by F_3 strains but not exceeded significantly.

Yields of F_2 plants on the average exceeded those of both parents at Bozeman but were less variable. Plant yields were studied in the F_3 generation at Bozeman where Marquis was the highest yielding parent and at Havre where Hard Federation was the highest yielding parent. From a high-yielding F_2 plant an F_3 strain was studied which significantly outyielded both the Marquis at Bozeman and the Hard Federation at Havre.

The crude-protein content of grain from F_2 plants was found intermediate between that of the parents and not significantly more variable. F_3 strains from the highest F_2 plants did not rank among the best crude-protein strains at Bozeman or Havre. High crude-protein F_3 strains were found less variable than low crude-protein strains. While strains of lower crude-protein content than Hard

Federation were obtained, no F_3 strain was studied which exceeded, although several practically equaled, Marquis in crude-protein content.

The product of average yield per plant and crude-protein content was used to measure the amount of improvement made over the parents. The six leading strains at Bozeman, Moccasin, and Havre exceeded the best Marquis check rows from 1.5 to 81.8 per cent. This improvement in yield × crude-protein content apparently was obtained by combining the advantages of the long fruiting period of Hard Federation and the height of Marquis.

The amount of correlation was determined between all of the six quantitative characters—heading period, ripening period, fruiting period, height, yield, and crude-protein content—at Bozeman, Moccasin, and Havre. The amount of correlated inheritance was found for each character in the F_2 and F_3 generations at Bozeman, and also in the F_2 generation at Bozeman with the F_3 generation at Havre.

Important and significant negative correlations were obtained between heading period and fruiting period and large positive correlations between ripening period and fruiting period.

The longer fruiting period and greater height were the most important factors positively correlated with larger yields.

Fruiting period, height, and yield were, on the average, all negatively correlated with crude-protein content.

Correlation between F_2 plants and F_3 strains, indicative of inheritance, were obtained in important significant amounts at Bozeman for heading period, height, and yield and at Moccasin for height and yield. Only one character, heading period, was inherited in a significant amount in F_3 strains at Havre in 1924 from their F_2 parent plants raised at Bozeman in 1923.

It is expected to develop, through the further testing of selections made on the basis of these studies, a new variety better adapted to Montana conditions than either Hard Federation or Marquis.

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